A MONOGRAPH OF LYONIA (ERICACEAE)[1]

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THE GENUS *Lyonia* Nuttall is an especially fascinating group and is of general biological interest. One is first confronted with the basic question of defining the genus, since *Lyonia* has often been confused with several related genera of the Andromedeae (Ericaceae), especially *Pieris* D. Don, and has sometimes been split into several genera. (This topic has been treated in Judd, 1979.) The genus has never been monographed, although there are various local studies (Small, 1914, 1933; Roig & Acuña, 1957; Handel-Mazzetti, 1936; Fernald, 1950; Anonymous, 1974). However, these treatments have done little to determine phenetic or phylogenetic relationships between taxa. Species of *Lyonia* recognized in the past have been based on characters that are extremely variable within single populations, and even in individual plants. This overdescription of both the West Indian and eastern Asian species has obscured several important ecological, geographic, and morphological patterns.

Lyonia is of phytogeographic interest since it has an eastern Asian–eastern North American disjunction, with an additional center of diversity in the Greater Antilles; one species also occurs in the mountains of eastern and southern Mexico. Therefore, questions concerning the phytogeographic relationships between Asia, eastern North America, Mexico, and the West Indies are discussed. The genus is intriguing from an evolutionary standpoint, since extensive speciation and adaptive radiation have occurred in the Greater Antilles (especially Cuba and Hispaniola), with species occurring at a wide range of elevations, on diverse soil types, and in various vegetation types. Most species of *Lyonia* in this region are narrowly endemic, and many have developed unusual morphological and/or anatomical characteristics.

Phenetic and phylogenetic studies of *Lyonia* and its relatives in the Andromedeae have reaffirmed the generic distinctiveness of *Lyonia* and have clarified relationships among such related genera as *Pieris* D. Don, *Craibiodendron* W. W. Smith, *Agarista* D. Don, and *Agauria* Hooker f. (Judd, 1979). The genus is most easily distinguished by the following characters (here listed in order of importance): prominently thickened capsule sutures; geniculate (or S-shaped) filaments often with two slender and partially disintegrating spurs near the apex; buds frequently with two imbricate scales; inflorescences that overwinter inside the bud; twigs usually with homogeneous pith; minute, wingless seeds with elongated testa cells; leaves with bifacial petiole and/or

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midrib bundles; multicellular hairs with biseriate stalks and large, swollen heads (or heads flattened to form peltate scales); and two more or less opposite bracteoles positioned at or near the base of the pedicel (for further details see Judd, 1979).

The species of *Lyonia* can be grouped into four sections that differ chiefly in structure of their multicellular hairs, in inflorescence type, and in several anatomical features. Sect. PIERIDOPSIS is limited to eastern Asia, sect. LYONIA is most diverse in the West Indies, and sects. MARIA and ARSENOCOCCUS are essentially limited to eastern North America. *Lyonia* is especially diverse in the Greater Antilles, with thirteen species (seventeen taxa) in Cuba, ten (eleven taxa) in Hispaniola, two in Jamaica, and a single one (but two taxa) in Puerto Rico and St. Thomas. Six species (seven taxa) are native to continental North America, and five (thirteen taxa) are found only in eastern Asia. Most species occur in rather sunny environments with acid soils, and species in the West Indies are often limited to mountainous areas.

In the Caribbean the genus has apparently undergone adaptive radiation on each island, with very little exchange of taxa between islands. Within an island the species are often limited to a single mountain range and are usually adapted to specific habitats. The habitats of the generalized species tend to be relatively mesic to slightly xeric, while those of the specialized species are more extreme (e.g., dry white-sand savannas, high-elevation pine forests, or thickets or pine-lands on deep lateritic soils rich in iron oxide, which are developed over serpentine). In the Cordillera Central of Hispaniola, there are pairs of related species (e.g., *Lyonia heptamera* and *L. buchii, L. tuerckheimii* and *L. rubiginosa, L. urbaniana* and *L. tinensis*) with one member in a high-elevation *Pinus occidentalis* forest and the other in a low-elevation pine forest, the two separated by a narrow band of cloud forest at ca. 2000 meters. This pattern is also seen in the Blue Mountains of Jamaica, where *L. octandra* occupies the cloud or elfin forests near the summits and the related *L. jamaicensis* grows on the southern slopes in dry forests at lower elevations. A few Cuban species are also isolated ecologically and altitudinally. Other taxa of Hispaniola (*L. urbaniana* and *L. microcarpa,* for example) are closely related but are geographically isolated because they occur in different mountain ranges. Many Cuban taxa (e.g., the varieties of *L. nipensis,* of *L. obtusa,* of *L. glandulosa,* and of *L. latifolia*) are also geographically isolated. A few species, such as *L. truncata* and *L. microcarpa* (or *L. ferruginea* and *L. fruticosa* of the southeastern United States), seem to be at least partially isolated because they flower at different times.

In contrast to the narrowly endemic species of the Greater Antilles, several species of eastern Asia and the United States (for example, *Lyonia ovalifolia, L. villosa,* and *L. ligustrina*) are very widespread and are usually composed of numerous geographic varieties. *Lyonia ovalifolia* occurs in an arc of over 3500 miles from Japan across China and the Himalayas to northern Pakistan and extends south as far as Thailand, Vietnam, and the Malay Peninsula. These species often spread vegetatively by horizontal underground rhizomes.

In the past six years over 9000 herbarium specimens have been studied, and natural populations of nearly all the taxa of North America, Hispaniola, Jamaica, and Puerto Rico have been investigated in detail. The species of Cuba and eastern Asia have had to be studied from herbarium material alone. The morphology, anatomy, systematics, ecology, cytology, and geographic distribution of each species have been investigated as thoroughly as possible.

Since the species of *Lyonia* had not been intensively studied in the field, and plants of various geographically or politically separated areas had not been critically compared, the species previously recognized were often highly artificial. The varieties of the widespread Asian species recognized here have often been considered to be distinct species, and slightly different morphological forms—or even identical but geographically separated populations—of the taxa of the West Indies have been similarly treated. These species were often based upon slight differences in leaf shape, the prominence of marginal serrations, or certain indumentum features, but these characters vary within single populations or even within an individual plant. However, many other useful characters such as epidermal lignification and cell shape, venation type, distribution of unicellular hairs, and variation in the morphology of the peltate scales were ignored.

Out of nearly 120 named taxa, 35 species (51 taxa)—including two species and two varieties described for the first time—are recognized here. The species recognized have distinct complexes of morphological characters, geographic ranges, and ecological characteristics.

INFRAGENERIC RELATIONSHIPS

Sectional Relationships

The genus *Lyonia* can be divided into four natural and morphologically distinctive groups, which are recognized in this treatment as sections (see Judd, 1979).

Lyonia sect. Pieridopsis includes *L. ovalifolia, L. villosa, L. chapaënsis, L. macrocalyx,* and *L. compta,* all natives of eastern Asia. These species are characterized by racemose inflorescences; an indumentum of multicellular, long-headed hairs; stems with homogeneous pith; entire-margined, persistent to deciduous leaves usually with unlignified epidermal cells; calyx lobes valvate in bud; filaments usually covered with long, unicellular hairs, at least near the base; two large, imbricate bud scales that often become reddish in autumn; capsules with thickened sutures that usually do not separate as a unit from the adjacent valves in dehiscence; and subapical to more or less central placentae. All of these species except *L. compta* have the floral buds located below the vegetative buds and lack a hypodermis in the leaves. The leaves of all species have bifacial midrib and petiole bundles, although the vascular tissue does not characteristically form a complete ring of xylem (as seen in cross section) within the petiole, as is common in *Lyonia* sect. Lyonia. All species probably spread vegetatively by horizontal underground rhizomes, although as yet this has been documented only for *L. ovalifolia* and *L. villosa.*

Lyonia ovalifolia, L. villosa, and *L. macrocalyx* are probably quite closely related, and all have capsules with more or less prominently thickened sutures, floral buds borne below the vegetative buds, more or less horizontal to slightly ascending racemes, and semipersistent to deciduous leaves; all lack a leaf hypodermis. *Lyonia compta* appears to be an isolated species that lacks thickened sutures and that has flower buds above the vegetative buds, more or less rigidly ascending racemes, and evergreen leaves with an unlignified adaxial hypodermis. *Lyonia compta* is more similar to the North American *L. ligustrina* in floral bud position and in corolla shape than is any other Asian species. (In *Lyonia* sects. MARIA and ARSENOCOCCUS the floral buds are always positioned above the vegetative buds. In *Lyonia* sect. LYONIA the two bud types are often mixed, but the floral buds tend to develop near the distal end of the branches.) *Lyonia chapaënsis* helps to ally this taxon with the other Asian lyonias, since it also essentially lacks thickened sutures and has very similarly shaped capsules, but has leaves that are morphologically and anatomically very similar to those of *L. ovalifolia.*

Lyonia sect. ARSENOCOCCUS includes the single species *L. ligustrina,* which is native to eastern North America. This taxon is characterized by flowers in complex, paniculate inflorescences; indumentum of multicellular, long-headed hairs; twigs with heterogeneous pith; clearly to only minutely serrulate-margined leaves usually with unlignified epidermal cells; calyx lobes valvate in bud; filaments with long, unicellular hairs near the base; two large, imbricate bud scales that often become reddish in autumn; capsules with thickened sutures that usually do not separate as a unit from the adjacent valves in dehiscence; and placentae positioned more or less subapically. *Lyonia ligustrina* commonly spreads vegetatively by horizontal underground rhizomes. The leaf-midrib bundle is bifacial but does not consistently form a cylinder of xylem within the petiole.

Lyonia sect. MARIA, as defined here, includes two rather distinctive species, *L. mariana* and *L. lucida.* Both are native to eastern North America, although *L. lucida* also occurs in western Cuba. This section is characterized by flowers in fascicles; indumentum of multicellular, short-headed hairs; twigs with homogeneous pith; entire-margined, deciduous (*L. mariana*) or persistent (*L. lucida*) leaves with unlignified or only slightly lignified epidermal cells; calyx lobes valvate in bud; filaments with long, unicellular hairs (*L. mariana*) or merely roughened (*L. lucida*); buds with 2 to 6 (to 8) imbricate scales; and more or less central to nearly basal placentae. The capsular sutures are always strongly thickened and occasionally separate as a unit from the adjacent valves. Both species have conspicuous spurs near the apex of the filaments and spread vegetatively by horizontal underground rhizomes. These two species, although isolated vegetatively, are placed in a single section because of their strong similarities in inflorescence and floral morphology. *Lyonia lucida* is distinctive vegetatively because of its strongly three-angled stems and its very coriaceous, persistent leaves with an intramarginal vein and a unifacial midrib bundle. However, occasional species in other sections (cf., for example, *L. buchii, L. heptamera, L. glandulosa, L. compta*) are anatomically or morphologically peculiar in a few characters, and the few primarily vegetative differences between *L. mariana* and *L. lucida* do not justify placing each in a monotypic section.

Lyonia sect. LYONIA is in many respects the most distinctive subgroup within the genus. It includes *L. ferruginea* and *L. fruticosa,* of the southeastern United States; *L. squamulosa,* of the mountains of eastern and southern Mexico; and 24 species of the Greater Antilles. These species are characterized by flowers in fascicles (or less commonly in short racemes); indumentum of multicellular, peltate scales; stems with a homogeneous pith; entire to irregularly serrate-margined, persistent leaves with epidermal cells strongly lignified (also often with hypodermis lignified); calyx lobes imbricate in bud; filaments merely roughened; buds with two rather small, imbricate bud scales; capsules with prominently thickened sutures usually separating as a unit from the adjacent valves in dehiscence; and more or less subapical placentae. The petiolar vascular bundle of all species is bifacial and characteristically forms a cylinder of xylem and phloem surrounded by a ring of fibers. Only *L. ferruginea, L. fruticosa,* and *L. squamulosa* are known to spread vegetatively by underground rhizomes.

The morphological diversity of this group has been underestimated in the past because of the incomplete knowledge of most of the Caribbean taxa. For example, the group is often said to lack spurs, but many Cuban species (e.g., *L. macrophylla, L. ekmanii, L. obtusa, L. nipensis*) have at least small spurs near the apex of the filament. The species of this group are said to bear their flowers in fascicles, but *L. heptamera* and *L. buchii* often have short racemes. Other peculiarities of the group and the relationships between its many species are discussed in detail below.

Sections PIERIDOPSIS, ARSENOCOCCUS, and MARIA all differ from sect. LYONIA in lacking ferrugineous, peltate scales and in having leaves with the epidermal cells only very occasionally lignified and only rarely with a hypodermis, and petiolar vascular tissue that does not consistently form a cylinder. In addition, species in these sections usually have long, unicellular hairs on their staminal filaments (vs. merely roughened filaments) and thickened sutures that only occasionally separate as a unit from the adjacent valves in dehiscence; they usually spread vegetatively by horizontal underground rhizomes. These three sections are probably more closely related to each other than to sect. LYONIA (see also Judd, 1979). Sections ARSENOCOCCUS and PIERIDOPSIS are especially close since both have an indumentum of characteristic long-headed, multicellular hairs (vs. short-headed hairs in sect. MARIA), but sect. MARIA is quite similar to some species of sect. PIERIDOPSIS in corolla and capsule shape, filament and spur morphology, and placenta position. Section PIERIDOPSIS tends to connect sects. ARSENOCOCCUS and MARIA, which would otherwise appear very distinctive. One could make a case for placing these three sections in one subgenus; a second subgenus would contain only species placed in sect. LYONIA (see Wood, 1961). This has not been done here since the only absolutely constant character distinguishing the two groups is the presence of peltate scales in *Lyonia* sect. LYONIA and their absence in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS. The sectional limits accepted here are thus the same as those of Rehder (1924) and Stevens (1969).

The various generic and infrageneric classifications of the species here considered in *Lyonia* are summarized in TABLE 1 (see also Judd, 1979).

TABLE 1. **Comparative treatment of Lyonia by various authors.**

	TAXA			
AUTHORS	**Lyonia** sect. **Arsenococcus**	**Lyonia** sect. **Pieridopsis**	**Lyonia** sect. **Maria**	**Lyonia** sect. **Lyonia**
Linnaeus (1753)	*Vaccinium*	—	*Andromeda*	—
Michaux (1803) Pursh (1814) Elliott (1817)	*Andromeda*	—	*Andromeda*	*Andromeda*
Nuttall (1818)	*Lyonia*	—	*Andromeda*	*Lyonia*
D. Don (1834)	*Lyonia*	*Pieris*	*Lyonia*	*Lyonia*
De Candolle (1839)	*Lyonia*	*Pieris* sect. 1	*Leucothoë* sects. *Maria, Euleucothoë*	*Lyonia*
Bentham & Hooker (1876)	*Lyonia* sect. 2	*Pieris* sect. *Eupieris*	*Pieris* sect. *Maria*	*Lyonia* sect. 1
Gray (1878)	*Andromeda* subg. *Lyonia*	*Andromeda* subg. *Pieris* (Asiatic subsect.)	*Andromeda* subg. *Pieris* subsect. *Maria*	*Andromeda* subg. *Lyonia*
Britton & Brown (1913)	*Xolisma*	—	*Neopieris*	*Xolisma*
Small (1914)	*Arsenococcus*	—	*Neopieris/ Desmothamnus*	*Xolisma*
Rehder (1924, 1927)	*Xolisma* sect. *Arsenococcus*	*Xolisma* sect. *Pieridopsis*	*Xolisma* sect. *Maria*	*Xolisma* sect. *Lyonia*
Wood (1961)	*Lyonia* sect. *Maria*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Lyonia*

PHYLOGENETIC ANALYSIS

Lyonia sect. LYONIA includes 27 species (34 taxa) and is very diverse in the Greater Antilles. The phylogenetic relationships in this section were investigated using the method of Wagner (1961, 1962, 1969). Thirty-two characters were used and assigned generalized and specialized states; TABLE 2 lists these characters. All taxa recognized were considered to be "Operational Taxonomic Units" (OTUs). For each of the characters, each OTU was scored 0 if generalized and 1 if specialized. When both generalized and specialized states of any given character were present in an OTU, that character was scored as "var." (variable) but was also scored as either 0 or 1, depending upon which was more common within—or characteristic of—that OTU. When two or more states of a given character are considered derived, each is given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). All of the OTUs are listed in TABLE 3, together with the character divergence values for each. The total divergence index of each taxon was determined by adding the individual divergence values of each character. Then mutual groupings of derived character states between taxa were determined, and the taxa were arranged according to these groupings. They were then plotted on a concentric

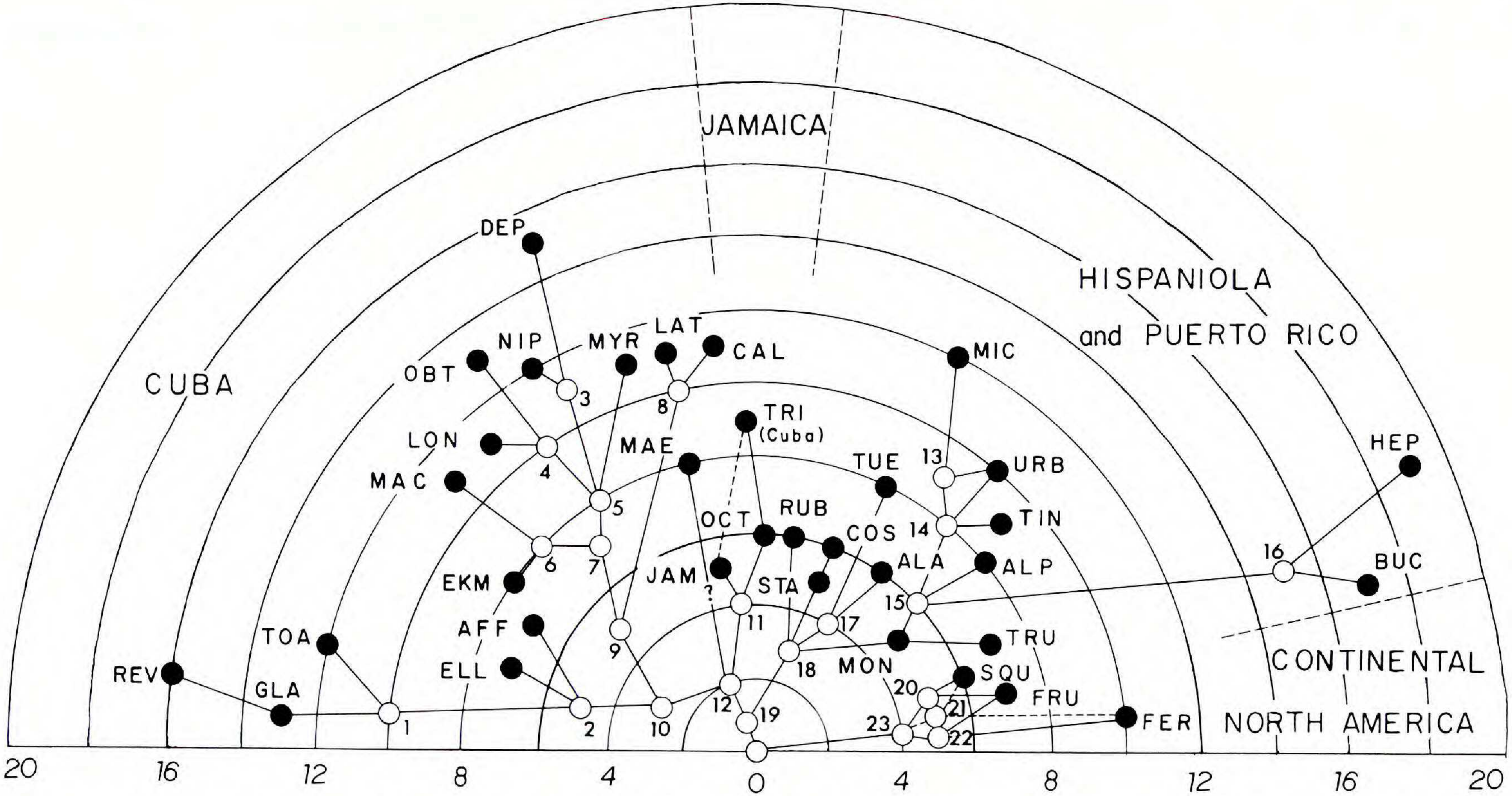

FIGURE 1. Wagner Tree for species and varieties of *Lyonia* sect. LYONIA: present-day taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles).

graph (FIGURE 1), the radii being determined by the mutual groupings of characters, and the distance from the center by the divergence of each OTU. Thus, only the branching points and the evolutionary divergence values (i.e., the length of the lines) indicated by this figure are meaningful.

As previously discussed (see Judd, 1979), the Wagner method requires that numerous assumptions be made regarding the derived and the generalized state of each character. These assumptions are often rather subjective and introduce a major source of both error and circular reasoning.

Characters in which the derived state could be determined by functional and/or ecological considerations (in conjunction with out-group comparison) include: B, C, G, I, M, N, S, T, Y, Z, AA, CC, and HH (TABLE 2). The dense covering of unicellular hairs on the abaxial leaf surface (G) of many species may be an adaptation to reduce water loss; species lacking this adaptation tend to grow in more mesic environments (such as cloud forests or moist montane forests), while taxa with it often grow in dryer oak-pine or pine savannas or thickets, although many exceptions occur. Similarly, taxa with strongly revolute leaves (I) tend to grow in extreme environments. Thus *Lyonia glandulosa* and *L. nipensis* var. *depressinerva* are found on the limonite plateau near Moa, Cuba. In such environments, taxa from many different families have convergently evolved this leaf morphology, and even within the Andromedeae such small and strongly revolute leaves are found in *Tepuia* Camp and in several Brazilian species of *Agarista* that grow in similar stressful habitats. Plants with rigidly ascending branches bearing reduced leaves (C) occur only in species adapted to very sunny and seasonally very dry habitats (i.e., usually savannas or open pine forests). This condition is possibly photosynthetically adaptive and is useful in reducing water loss or overheating due to solar radiation (Horn, 1975; Gates, 1968). Some species such as *L. urbaniana, L. microcarpa,* and *L. alpina* characteristically have a dense covering of long-stalked, ferrugineous scales (M, N) on their leaves, and the first two have their stomata sunken into pockets formed in the lower leaf surface by the densely raised-reticulate (S) veins. These species also always have a dense layer of unicellular hairs on their abaxial leaf surfaces. This complex of characters usually occurs in taxa growing in rather high elevations and is probably of adaptive significance. Such high-elevation species are also often densely branched shrubs with fairly small leaves. The presence of strongly depressed leaf veins (T) is characteristic of many taxa of stressful environments (i.e., dry, sterile sands or lateritic soils over serpentine) and may affect the physiological functioning of the leaf. The presence of 7-, 6-, (or 4-)merous flowers (Y) is possibly due to selection for larger (or smaller) flowers; unfortunately, the pollination biology of the Caribbean species has not been well studied. The shape and pubescence of the corolla (Z, AA) and the presence of filament spurs (CC) may also be related to the pollination biology of the species. The presence of spurs in many of the Cuban species was considered to be a generalized condition because the spurs are morphologically identical to those present in many species of sects. PIERIDOPSIS, MARIA, and ARSENOCOCCUS. Spurs have been lost independently in several Asian and the majority of West Indian species. Finally, some species of higher elevations

TABLE 2. **Characters used in phylogenetic study* of Lyonia sect. Lyonia.**

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Plants producing rhizomes	Yes	No
B	Habit	Moderate-sized to small shrubs	Sometimes large trees
C	Ultimate branchlets	Not rigidly ascending; leaves not reduced near tips	At least sometimes rigidly ascending; leaves reduced in size
D	Stem pubescence (unicellular hairs)	Lacking hairs to moderately covered with them	At least sometimes densely pubescent
E	Presence of short, unicellular hairs on midvein of adaxial leaf surface	Yes	No
F	Short, unicellular hairs on midvein of abaxial surface of leaves	Lacking	Often present (at least at base)
G	Abaxial leaf surface with a dense layer of unicellular hairs	No	Yes
H	Texture of adaxial leaf surface	± Smooth	At least sometimes roughened (persistent bases of peltate scales)
I	Leaf margin strongly revolute	No	Yes
J	Peltate scales (abaxial leaf surface)	± One type	Two distinct morphological types
K	Marginal dentation of leaf	± Entire to obscurely toothed	Often strongly and irregularly toothed
L	Color of peltate scales (on leaves)	Rusty, reddish	a. ± Golden b. Light to dark brown
M	Density of peltate scales on leaf surfaces	Sparse to moderate	Often dense

TABLE 2 (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
N	Stalks of peltate scales ± sunken into abaxial leaf epidermis	Yes	No
O	Length of petiole	Short to moderate	Often elongated (> 10 mm.)
P	Leaf base	Cuneate to rounded or attenuate	Cordate
Q	Leaf apex	At least sometimes acuminate	Acute, obtuse, rounded, or truncate
R	Distribution of unicellular hairs on petiole	Limited to adaxial surface	a. Completely lacking b. Often or sometimes covering all surfaces
S	Venation of leaves (abaxial surface)	Veins ± obscure to laxly reticulate; lacunae lacking	a. Veins coarsely raised-reticulate; lacunae present b. Veins finely raised-reticulate; lacunae present
T	2° veins on adaxial leaf surface usually depressed	No	Yes
U	Petiole anatomy	Medullary bundles lacking	Several medullary bundles present
V	2° and 3° veins of leaf (as seen in cross section)	Transcurrent	a. Semitranscurrent b. Embedded
W	Leaf hypodermis	Strongly to at least partially developed	Lacking
X	Epidermal lignification of leaves	Cells ± uniformly lignified	Cells with inner periclinal walls strongly thickened and lignified
Y	Number of flower parts	5 per whorl	a. 6 or 7 per whorl b. 4 per whorl

Z	Size and shape of corolla	Medium sized, ± cylindrical	a. Shortly urceolate to globose b. Elongate-urceolate c. Minute and ± cylindrical or slightly urceolate d. Large (> 7 mm. wide), urceolate e. Large (> 7 mm. wide), campanulate
AA	Density of peltate scales on corolla	± Sparse	± Dense
BB	Length of calyx lobes	Short (< 2 mm.)	Long (often 3–4 mm.)
CC	Filament spurs	± Well developed	Lacking or minute
DD	Shape of capsules	Ovoid to ellipsoid	a. Urn shaped b. ± Subglobose c. Narrowly ovoid d. Minute, extremely narrowly ovoid or ellipsoid e. Very large, subglobose to short-ovoid
EE	Pedicels elongated in fruit	No	Yes
FF	Flower articulated with pedicel	Yes	No
GG	Capsules often with thickened ridge (resembling suture) running down center of each valve	No	Yes
HH	Twigs (thickness)	Usually ± slender	Very stout
II	Calyx lobes densely covered with peltate scales on adaxial surface	No	Yes

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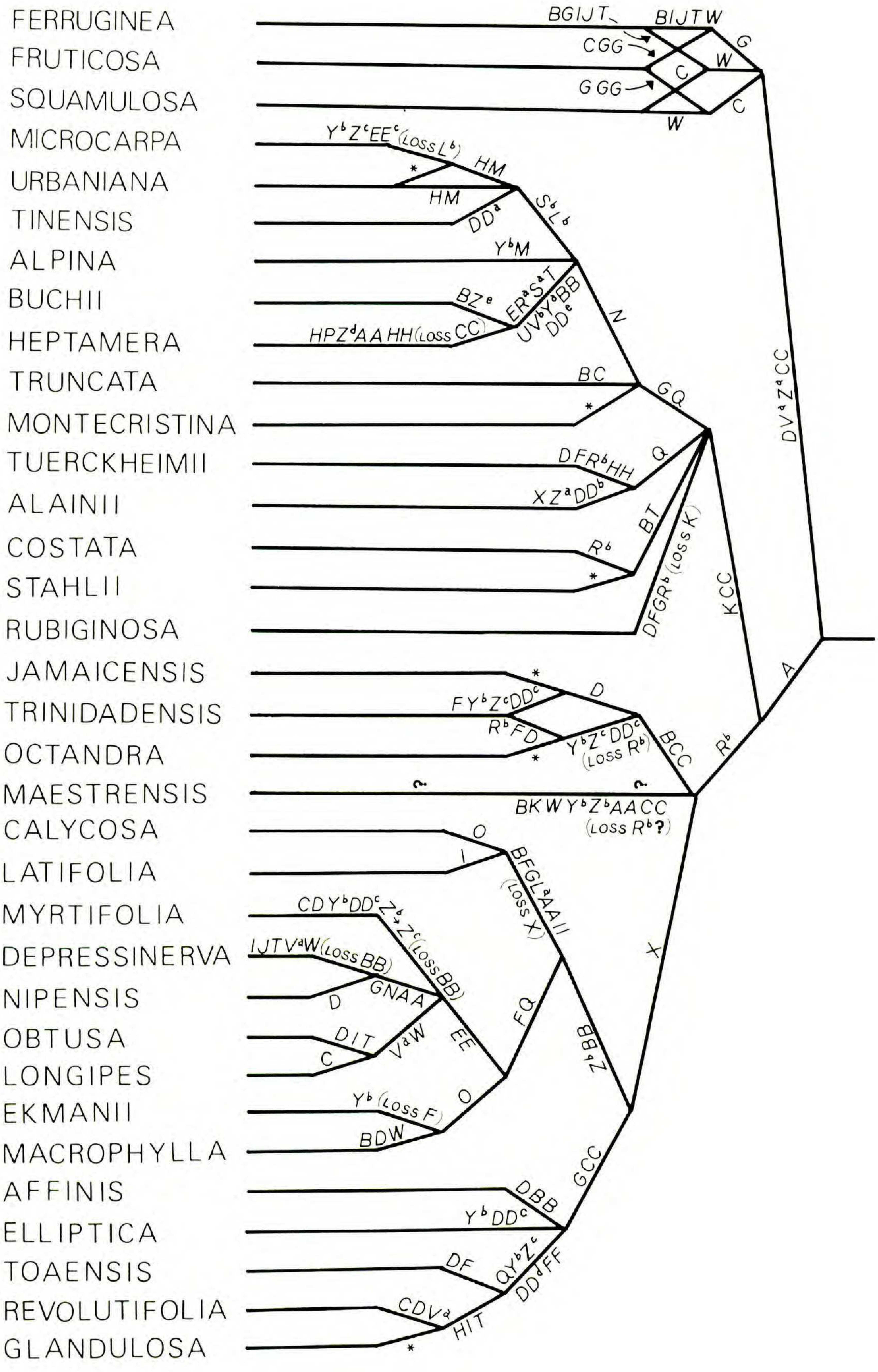
*Wagner Method.


FERRUGINEA
FRUTICOSA
SQUAMULOSA
MICROCARPA
URBANIANA
TINENSIS
ALPINA
BUCHII
HEPTAMERA
TRUNCATA
MONTECRISTINA
TUERCKHEIMII
ALAINII
COSTATA
STAHLII
RUBIGINOSA
JAMAICENSIS
TRINIDADENSIS
OCTANDRA
MAESTRENSIS
CALYCOSA
LATIFOLIA
MYRTIFOLIA
DEPRESSINERVA
NIPENSIS
OBTUSA
LONGIPES
EKMANII
MACROPHYLLA
AFFINIS
ELLIPTICA
TOAENSIS
REVOLUTIFOLIA
GLANDULOSA
BGIJT
BIJTW
CGG
GGG
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$Y^bZ^cEE^c$(LOSS L^b)
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S^bL^b
Y^bM
BZ^e
ER^aS^aT
UV^bY^aBB
DD^e
HPZ^dAAHH(LOSS CC)
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XZ^aDD^b
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R^b
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$DFGR^b$(LOSS K)
KCC
DV^aZ^aCC
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$CDY^bDD^cZ^b_*Z^c$(LOSS BB)
$IJTV^aW$(LOSS BB)
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GNAA
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C
V^aW
EE
FQ
Z^bBB
Y^b(LOSS F)
O
BDW
GCC
DBB
Y^bDD^c
DF
QY^bZ^c
DD^dFF
CDV^a
HIT
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(such as *L. tuerckheimii* or *L. heptamera*) have stouter twigs (HH) and are shorter shrubs (B) than their relatives at lower altitudes. These characteristics have evolved independently in several evolutionary lines in response to the similar climatic factors facing plants of high elevations.

The derived states of many characters (A, B, E, F, H, L, M, N, O, P, R, S, U, V, W, Z, AA, BB, DD, EE, FF, GG, HH, II) were chosen, at least in part, because the condition was unusual within *Lyonia* sect. LYONIA (in-group comparison). It is admitted that the criterion of "uncommonness" cannot be defended, since the distribution of character states depends upon the phylogeny of the group and on where within this sequence a particular character changes (Stevens, 1980). Thus, this criterion was often used in conjunction with the preceding and/or the following ones. The derived states of the characters A, E, G, H, S, T, U, Y, FF, and GG were chosen, at least in part, because the condition was limited to one section of the genus (out-group comparison). Finally, a few character states (D, H, J, K, O, Q, X) were considered to be derived because they were correlated with other derived character states.

The Wagner tree resulting from the above procedure (FIGURE 1) indicates that the species of *Lyonia* sect. LYONIA belong to three major phyletic groups, with a small fourth group intermediate between two of these. (The derived character states of each OTU are shown in FIGURE 2.) The first is here called the Cuban group because all the taxa within it are native to either Cuba or the Isle of Pines. Only two Cuban species, *L. trinidadensis* and possibly *L. maestrensis*, have their greatest affinities with species of other islands. The Cuban group is composed of three related evolutionary lines, which are for convenience termed the *L. glandulosa* line (GLA), the *L. obtusa–L. nipensis* line (OBT-NIP), and the *L. latifolia* line (LAT). The second major evolutionary group is called the Hispaniolan group because all the taxa within it are native either to Hispaniola or to the adjacent islands of Puerto Rico and St. Thomas. It is composed of two subgroups, the *L. tuerckheimii* "line" (TUE), and the *L. microcarpa–L. truncata–L. heptamera* line (MIC-TRU-HEP). *Lyonia jamaicensis* and *L. octandra*, both native to Jamaica, along with *L. trinidadensis*, endemic to Las Villas Province, Cuba, form a small group of species intermediate between the larger Cuban and Hispaniolan species groups. The position of *L. maestrensis* is in doubt because mature capsules and flowers of this species have not been seen. It may be related to *L. latifolia*, since it appears, from the material now available, to have similarly shaped, densely lepidote corollas. However, it has distinctly toothed leaves, which may indicate a relationship with some of the more generalized species of the Hispaniolan group. The third major phylogenetic

FIGURE 2. Phylogenetic diagram for species and varieties of *Lyonia* sect. LYONIA showing derived characteristics of each taxon and evolutionary line. Newly acquired derived character states shown for each branching point (length of lines has no evolutionary meaning). Each taxon placed at end of line because extant species probably not directly ancestral to any others.

group has only three species (*L. ferruginea, L. fruticosa,* and *L. squamulosa*) and is limited to continental North America. It is called the North American group.

The species of the North American group all have stems at least sometimes densely pubescent (D), fibers surrounding the leaf veins usually not forming girders between the adaxial and abaxial leaf epidermis (V^a), and shortly urceolate corollas (Z^a); all lack prominent spurs on their filaments (CC) (FIGURE 2). The group is especially distinctive in its ability to spread vegetatively by horizontal underground rhizomes, which arise from large, woody, elongated burls, and in its characteristic shortly urceolate flowers. No other species of sect. LYONIA spreads vegetatively, and only *Lyonia alainii* has similarly shaped corollas.

Nearly all the Cuban taxa have petioles at least sometimes densely pubescent on all surfaces (R^b) and leaves in which the inner periclinal walls of the epidermal cells are especially strongly thickened and lignified (X). Within this group, *Lyonia affinis* and *L. elliptica* are the least specialized, but even these taxa are advanced in their lack of filament spurs (CC) and in the dense layer of unicellular hairs covering their abaxial leaf surfaces (G).

The *Lyonia glandulosa* evolutionary line in Cuba has developed the added specializations of leaf apices never acuminate (Q), 4-merous flowers (Y^b) with extremely small corollas (Z^c), and extremely narrowly ovoid to ellipsoid capsules (DD^b) lacking a visible articulation (FF) with the pedicel. The most advanced taxon of this phylogenetic group, *L. glandulosa* var. *revolutifolia,* also has strongly revolute leaves (I) with depressed veins (T). The above-mentioned characters make *L. toaënsis* and *L. glandulosa* among the more easily recognized of the Cuban species.

Most of the taxa of the *Lyonia obtusa–L. nipensis* evolutionary line are characterized by petioles often with unicellular hairs on all surfaces (R^b); leaves without acuminate apices (Q) but with epidermal cells having prominently thickened and lignified inner periclinal walls (X), and with short, unicellular hairs often present on the midvein of the lower surface (F); elongate-urceolate corollas (Z^b); and often elongated calyx lobes (BB). Within this group, *L. ekmanii* and *L. macrophylla* are probably closely related, and both characteristically have leaves with elongated petioles (O). It is interesting that the leaves of *L. macrophylla* lack a hypodermis, while those of *L. ekmanii* have one. *Lyonia macrophylla* also differs from *L. ekmanii* in its more consistently 5-merous capsules and its more densely pubescent twigs. The remaining taxa of the *L. obtusa–L. nipensis* line all have the pedicel of the fruit at least sometimes elongated (EE). Among these taxa, *L. myrtilloides* is rather isolated and is distinguished by often rigidly ascending branches bearing very small leaves (C), more or less densely pubescent stems (D), 4-merous flowers (Y^b), very small corollas (Z^c), and narrowly ovoid capsules (DD^c). *Lyonia nipensis* is distinguished by additional derived character states: abaxial leaf surface with a dense covering of unicellular hairs (G), stalks of peltate scales not sunken into abaxial epidermis (N), and densely lepidote corollas (AA). *Lyonia nipensis* var. *depressinerva* has several distinctive vegetative modifications, such as two types of peltate scales (J), and strongly revolute leaves (I) with depressed veins (T) and various anatomical pecularities (W, V^a). *Lyonia obtusa* is characterized by the lack of a hypodermis (W) and by the lignified sheaths of its leaf veins (V^a). *Lyonia obtusa* var. *obtusa* sometimes has strongly revolute leaves with clearly depressed major veins. There are several examples of parallel evolution of characters between these two species, which are evidently very closely related.

The *Lyonia latifolia* phylogenetic line, which is very distinctive (especially in floral morphology), is probably an offshoot from extinct primitive members of the Cuban group. *Lyonia latifolia* vars. *latifolia* and *calycosa* are distinguished by the following additional derived character states: sometimes arborescent habit (B); leaves with a dense covering of unicellular hairs on the abaxial surface (G), with short, unicellular hairs at least sometimes present on the midvein of the abaxial surface (F), and golden-colored, peltate scales (L^a); elongated calyx lobes with the adaxial surface densely covered by peltate scales (II); and elongate-urceolate (Z^b), densely lepidote (AA) corollas. *Lyonia latifolia* has uniformly lignified epidermal cells, an unusual characteristic among Cuban species.

With respect to the two remaining species that are endemic to Cuba, the relationships of *Lyonia maestrensis* are essentially unknown, while *L. trinidadensis* is undoubtedly more closely related to the Jamaican *L. octandra* and *L. jamaicensis* than it is to any other Cuban species. These three species form a small, rather nondescript group intermediate between the Cuban and Hispaniolan groups. They are characterized by their arborescent habit (B), petioles often covered on all surfaces with unicellular hairs (R^b) (lost in *L. octandra*), and filaments without well-developed spurs (CC). *Lyonia octandra* and *L. trinidadensis* have the additional specializations of small (Z^c), 4-merous (Y^b) flowers and narrowly ovoid capsules (DD^c).

Nearly all the species of Hispaniola and Puerto Rico are characterized by having at least sometimes strongly toothed leaves (B) and by lacking well-developed filament spurs (CC). The *Lyonia tuerckheimii* group includes a rather generalized assortment of taxa united more by their primitive traits than by any shared derived characters. All taxa lack unicellular hairs on the abaxial leaf surface (except some plants of *L. rubiginosa* var. *rubiginosa*), have obscure to laxly reticulate leaf veins, and are more or less sparsely to moderately lepidote. Several taxa at least occasionally have acuminate-tipped leaves. It is interesting that three of the five taxa comprising this group (*L. rubiginosa* vars. *costata* and *stahlii*, and *L. alainii*) often occur in cloud forests. The more generalized taxa within the group (e.g., *L. rubiginosa*) grow at low altitudes, while the more specialized *L. tuerckheimii* has become adapted to high-elevation pine forests. *Lyonia tuerckheimii* is distinctive in having densely pubescent (D), stout (HH) twigs; short, unicellular hairs on the midvein of the abaxial leaf surface (F); petioles at least sometimes with unicellular hairs on all sides (R^b); rigidly coriaceous leaves; and a rounded, "compact" habit.

The species of the *Lyonia microcarpa–L. truncata–L. heptamera* evolutionary line are all distinguished by the following additional derived characters: leaves not acuminate tipped (Q) but with a dense layer of unicellular hairs on the abaxial surface (G). The more generalized taxa, such as *L. truncata* vars. *montecristina* and *truncata,* occur at lower elevations than the more advanced ones (*L. alpina, L. tinensis, L. urbaniana, L. microcarpa,* and *L. heptamera*). *Lyonia tinensis, L. microcarpa,* and *L. urbaniana* are distinctive in that their leaves have a densely and finely raised-reticulate network of veins on the lower surface (S^b). The stomata of these species are present chiefly in the cavities formed in the abaxial surface by the raised-reticulate veins, and the stalks of their peltate scales are not sunken into the leaf epidermis (N). *Lyonia microcarpa* and *L. urbaniana* also have densely lepidote (M), very small leaves. *Lyonia buchii* and *L. heptamera* probably evolved from an extinct and generalized taxon of this phylogenetic line. They are extremely specialized, are thus distinctive in both floral and vegetative characters, and form a distinctive evolutionary grade. They have petioles lacking unicellular hairs (R^a) and with medullary bundles within the xylem cylinder (U); leaf veins with a distinctive lignified sheath (V^b), very strongly and coarsely raised and reticulate on the abaxial surface (S^a), slightly depressed on the adaxial (T); 6- or 7-merous flowers (Y^a); elongated calyx lobes (BB); and very large, subglobose to shortly ovoid capsules (DD^c). *Lyonia heptamera* is the only Hispaniolan species that sometimes has well-developed spurs on its filaments, and *L. buchii* is unique in its very widely urceolate to campanulate corollas.

Many examples of parallel evolution can be found among the various phylogenetic groups discussed above. These can be determined from FIGURE 2 and TABLE 3. One of the most interesting is the loss of filament spurs by most of the species of sect. LYONIA. Others are the development of an arborescent habit; densely pubescent stems; small leaves; abaxial leaf surface densely covered with unicellular hairs (note: the presence or absence of these hairs seems to be quite inconstant in a few generalized species), or with peltate scales with stalks not impressed into the epidermis; adaxial leaf surface roughened and with depressed secondary veins; leaf margin strongly revolute; the loss of a leaf hypodermis; 4-merous flowers with small corollas; and narrowly ovoid, 4-merous capsules.

The three major phyletic groups and their various subgroups are not given formal taxonomic recognition because of the small phenetic distance between the extant generalized species (e.g., *Lyonia affinis, L. ekmanii, L. jamaicensis, L. rubiginosa, L. truncata*).

Finally, one should not try to judge specific limits from FIGURES 1 and 2 because the frequency of individuals intermediate between any two OTUs and the nature of the characters separating them were not taken into account. For example, *Lyonia nipensis* var. *nipensis* and *L. nipensis* var. *depressinerva* appear to be widely separated in number of derived characters, while *L. tinensis* and *L. urbaniana* appear to be very similar. It is true that the extreme forms of the two varieties of *L. nipensis* appear more different than do *L. urbaniana* and *L. tinensis,* but there is a consistent morphological gap in the complex of characters defining the latter two species, while the characters distinguishing the varieties of *L. nipensis* are extremely variable, with more or less intermediate plants existing. In addition, the varieties of *L. nipensis* differ only in vegetative characters that are frequently rather variable within related species, while *L. tinensis* and *L. urbaniana* differ not only vegetatively but also in several flower and fruit characters.

EVOLUTION AND DISTRIBUTION

The 35 species of *Lyonia* recognized here are divided into four sections. Section PIERIDOPSIS, comprising five species, occurs in eastern Asia in an arc from northern Pakistan to Japan, and south to the Malay Peninsula. The greatest diversity of the genus, although not the greatest number of species, is in eastern North America, where three sections are represented. Section ARSENOCOCCUS, including the single species *L. ligustrina,* is found only in the eastern United States, in the Coastal Plain, Piedmont, and Appalachian and Ozark mountains. Section MARIA, comprising *L. mariana* and *L. lucida,* occurs in the Coastal Plain of eastern North America. *Lyonia lucida* is also native to Cuba (Pinar del Río and the Isle of Pines). Section LYONIA is the largest subgroup in the genus, containing 27 species. All of these except *L. ferruginea* and *L. fruticosa* (of the southeastern United States) and *L. squamulosa* (of the mountains of eastern and southern Mexico) are native to the Greater Antilles, occurring mostly in the mountains.

Lyonia is an ancient genus and was probably widely distributed in the mesophytic forests that once extended around the globe in northern regions. The characteristic assemblage of taxa in these forests has often been called the Arcto-tertiary Geoflora (Chaney, 1947). However, Wolfe (1969, 1975) has suggested that the concept of a geoflora is faulty. In 1969 he wrote, "it is extremely improbable from the genetic and physiological viewpoint that many lineages could have remained in association throughout the Tertiary." This may well be true but does not alter the fact that the antiquity of *Lyonia* is illustrated by its Tertiary relict disjunction pattern between eastern North America and eastern Asia, a distribution pattern first brought to the attention of American and European scientists by Asa Gray (Wood, 1972). This disjunction is made even more obvious when the phylogenetic relationships within *Lyonia* are considered. *Lyonia ligustrina* (sect. ARSENOCOCCUS) is probably more closely related to the Asian species (sect. PIERIDOPSIS) than it is to any other species of North America or the Caribbean region. However, sect. MARIA is also phyletically closer to the Asian species than it is to the West Indian species of the genus (sect. LYONIA). Many other genera show disjunction patterns similar to that shown by the group *Lyonia* sects. ARSENOCOCCUS, MARIA, and PIERIDOPSIS, and within the Ericaceae some examples are *Elliottia* (Bohm *et al.,* 1978), *Pieris* (Judd, 1981), *Epigaea, Menziesia, Leucothoë,* and various sections of *Gaultheria* and *Rhododendron* (Li, 1952; Wood, 1972). Paleobotanical findings have shown that genera, especially the woody ones, showing this pattern once occurred over wide areas from which they are now missing. The extant representatives of these genera are descendents of the survivors of the gradual climatic deterioration, volcanism, orogenic activity, and glaciation that have occurred since the mid-Tertiary (Li, 1952).

TABLE 3. **Character divergence values for each taxon used to construct Wagner Tree.***

CHARACTER	TAXA																																	
	GLA	REV	TOA	LAT	CAL	MAE	AFF	MAC	EKM	OBT	LON	NIP	DEP	MYR	TRI	OCT	JAM	RUB	STA	ELL	COS	ALA	TUE	TRU	MON	TIN	URB	MIC	ALP	BUC	HEP	SQU	FER	FRU
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
B	0	0	0	1	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0
C	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
D	0	1	1	0	0	0	1	1	0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
F	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
G	1	1	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1
H	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
I	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
J	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
K	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
L	0	0	0	1A	1A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	0	0	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
N	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0
O	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Q	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0
R	1B	1B	1B	1B	1B	0	1B	1B	1B	1B	1B	1B	1B	1B	1B	0	1B	1B	0	1B	1B	0	1B	0	0	0	0	0	0	1A	1A	0	0	0
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	1B	0	1A	1A	0	0	0

	GLA	REV	TOA	LAT	CAL	MAE	AFF	MAC	EKM	OBT	LON	NIP	DEP	MYR	TRI	OCT	JAM	RUB	STA	ELL	COS	ALA	TUE	TRU	MON	TIN	URB	MIC	ALP	BUC	HEP	SQU	FER	FRU
T	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
V	0	1A	0	0	0	0	0	0	0	1A	1A	0	1A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	1A	1A	1A
W	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
X	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Y	1B	1B	1B	0	0	1B	0	0	1B	0	0	0	0	1B	1B	1B	0	0	0	1B	0	0	0	0	0	0	0	1B	1B	1A	1A	0	0	0
Z	1C	1C	1C	1B	1B	1B	0	1B	1B	1B	1B	1B	1B	1C	1C	1C	0	0	0	0	0	1A	0	0	0	0	0	1C	0	1E	1D	1A	1A	1A
AA	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
BB	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
CC	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
DD	1D	1D	1D	0	0	0	0	0	0	0	0	0	0	1C	1C	1C	0	0	0	1C	0	1B	0	0	0	1A	0	1C	0	1E	1E	0	0	0
EE	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FF	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
HH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
II	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL	13	16	12	11	11	8	7	11	8	13	11	12	15	11	9	6	5	6	5	7	6	7	8	7	5	9	10	12	8	17	19	6	10	7

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*Each taxon is abbreviated by the first three letters of its name.

The species of *Lyonia* sect. LYONIA show disjunction patterns between the southeastern U. S. Coastal Plain, the montane areas of eastern and southern Mexico, and the islands of the Greater Antilles. There are many similarities between the deciduous forest formations of the eastern United States and the montane temperate forests of Mexico. Several species show disjunct distributions in these two areas, and a number of species pairs have representatives in the two regions (see Miranda & Sharp, 1950; Dressler, 1954; Martin & Harrell, 1957; Graham, 1964, 1973; Rzedowski, 1965; Gómez-Pompa, 1973). This eastern North American-Mexican relationship is illustrated by *L. ferruginea* and *L. fruticosa,* which occur on the Coastal Plain of South Carolina, Georgia, and Florida, and which are extremely closely related to *L. squamulosa,* of the Sierra Madre Oriental of Mexico. These three taxa are more closely related to each other than to any of the species of this section in the Greater Antilles.

Some authorities (e.g., Dressler, 1954) believe that the Mexican-eastern North American species migrated to Mexico during periods of ice advance; others (e.g., Braun, 1955; Martin & Harrell, 1957) contend that temperate plants reached Mexico at least by the middle of the Cenozoic. Recent palynological studies on Cenozoic deposits in Veracruz reveal a distinct and diverse arborescent temperate community already present in eastern Mexico by middle Miocene times, and collective data on the history of temperate trees and shrubs throughout northern Latin America demonstrate progressive independent southward migration of these elements (Graham, 1972, 1973). Thus, the floristic relationships between the eastern United States and eastern Mexico (and between *Lyonia ferruginea, L. fruticosa,* and *L. squamulosa*) may have had their origin in Tertiary rather than Pleistocene time.

Before the relationships of the Caribbean taxa are discussed, the geology and palynology of this area should be outlined briefly. Although numerous land bridges have been postulated between either Central or North America and the West Indies, these areas were probably never connected (MacGillavry, 1970; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972; Graham, 1972). During the Early Cretaceous, probably only a few volcanic peaks were emergent in the Caribbean (Graham, 1972), and until the end of the Cretaceous, numerous small islands continued to characterize the region (MacGillavry, 1970; Graham, 1972; Malfait & Dinkelman, 1972; Graham & Jarzen, 1969). After the late or middle Eocene, western and central Cuba were uplifted and remained an emergent stable platform. Cuba is thus the oldest of the West Indian islands, with Hispaniola and Puerto Rico being younger, and the Lesser Antilles the youngest of all (Malfait & Dinkelman, 1972; Nagel, 1971). By the Oligocene, there was extensive land area within the Caribbean, probably considerably greater than that existing today, and by late Miocene time, the islands of the Greater Antilles had essentially attained their modern aspect (Malfait & Dinkelman, 1972; Graham, 1972; Graham & Jarzen, 1969). It has become apparent from recent palynological studies of the San Sebastian formation of Puerto Rico that the Oligocene vegetation of the island was similar in generic composition to the modern Antillean flora. Among the 44 pollen and spore types found, 31 represent genera now growing in Puerto

Rico (Graham & Jarzen, 1969; Graham, 1972). Graham and Jarzen (1969) have postulated (and there is geologic evidence in support) that the Caribbean land mass of the Oligocene, in addition to being larger than at present (including Hispaniola, Puerto Rico, and the Virgin Islands), was also higher, having reached elevations of 13,000 to 15,000 feet. This would account for the presence in the San Sebastian flora of pollen of *Fagus* L., *Liquidambar* L., and *Nyssa* L., which indicates that an arborescent, cool-temperate community existed. These genera may have migrated into the Oligocene highlands and into the mountains of eastern Mexico at about the same time. There is evidence of the lowering of these highlands through both subsidence and rapid erosion (Graham, 1972; Graham & Jarzen, 1969).

Several genera of Pinar del Río, Cuba, may have reached the Caribbean from the north (i.e., from the southeastern United States). Some of these are *Kalmia* L., *Pieris, Quercus* L. (but see Borhidi & Muñiz, 1971), *Fraxinus* L., and *Pinus* L. (see Howard, 1973, and Alain, 1958). *Lyonia lucida* (sect. Maria) shows this pattern since it is widespread on the Coastal Plain of

Table 4. **Distribution of taxa among the major mountain ranges of Hispaniola.**

I. Cordillera Central–Massif du Nord (8 taxa)

Lyonia rubiginosa var. *costata*
L. tuerckheimii
*L. alainii**
L. truncata var. *montecristina**
*L. tinensis**
*L. urbaniana**
L. buchii
*L. heptamera**

II. Massif de la Selle–Sierra de Baoruco (6 taxa)

L. rubiginosa var. *costata*
L. tuerckheimii
L. truncata var. *truncata**
*L. alpina**
*L. microcarpa**
L. buchii

III. Sierra de Neiba (1 taxon)

L. rubiginosa var. *costata*

IV. Massif de la Hotte (1 taxon)

L. rubiginosa var. *costata*

V. Massif des Cahos (1 taxon)

L. buchii

*Taxon endemic to mountain range; see Map 2.

TABLE 5. **Distribution of taxa among the major mountain ranges of Cuba.**

I. Sierra de Cristal–Sierra de Mícara (5 taxa)
  - *Lyonia nipensis* var. *nipensis*
  - *L. obtusa* var. *longipes**
  - *L. macrophylla*
  - *L. glandulosa* var. *revolutifolia*
  - *L. latifolia* var. *calycosa* (rare)

II. Sierra Maestra (including Gran Piedra) (4 taxa)
  - *L. affinis**
  - *L. maestrensis**
  - *L. latifolia* var. *latifolia** (Loma del Gato and westward)
  - *L. latifolia* var. *calycosa* (Loma del Gato and eastward)

III. Sierra de Nipe (3 taxa)
  - *L. nipensis* var. *nipensis*
  - *L. macrophylla*
  - *L. glandulosa* var. *glandulosa**

IV. Moa Plateau (3 taxa)
  - *L. nipensis* var. *nipensis*
  - *L. macrophylla*
  - *L. glandulosa* var. *revolutifolia*

V. Sierra de Moa–Sierra de Toa (4 taxa)
  - *L. nipensis* var. *depressinerva**
  - *L. obtusa* var. *obtusa*
  - *L. macrophylla*
  - *L. glandulosa* var. *revolutifolia*

VI. Baracoa region (2 taxa)
  - *L. obtusa* var. *obtusa*
  - *L. macrophylla*

VII. Monte Libanon (1 taxon)
  - *L. nipensis* var. *nipensis*

VIII. Sierra de Imías–Alto de Iberia (1 taxon)
  - *L. latifolia* var. *calycosa*

IX. Sierra de Frijol (Pico Galano) (1 taxon)
  - *L. toaënsis**

X. Pinar del Río–Isla de Pinos (3 taxa)
  - *L. lucida*
  - *L. ekmanii**
  - *L. myrtilloides**

XI. Monte Verde–Monte Toro (1 taxon)
  - *L. elliptica**

TABLE 5 (*continued*).

XII. SIERRA DE TRINIDAD–SIERRA DE SANCTI SPIRITUS (1 taxon)
*L. trinidadensis**

*Taxon endemic to mountain range; see MAP 1.

the southeastern United States and occurs disjunctly in Pinar del Río and the Isle of Pines.

Lyonia sect. LYONIA is extremely diverse in the West Indies, with twelve species (sixteen taxa) occurring in Cuba, ten (eleven taxa) in Hispaniola, two in Jamaica, one in Puerto Rico, and one in St. Thomas. With the exception of *L. rubiginosa,* all these species are endemic to a single island. *Lyonia rubiginosa* occurs on three islands but has differentiated into three geographically isolated varieties: var. *costata* on Hispaniola, var. *stahlii* on Puerto Rico, and var. *rubiginosa* on St. Thomas.

Within the Greater Antilles, *Lyonia* shows a "Western Continental" distribution pattern (see Asprey & Robbins, 1953; Alain, 1958; Howard, 1973). Genera with this pattern are missing from the Lesser Antilles, are often most diverse in Cuba, and decrease in diversity eastward to the Virgin Islands. Thus, of the thirty Caribbean taxa of *Lyonia,* sixteen are endemic to Cuba, eleven to Hispaniola, two to Jamaica, and one to Puerto Rico. These genera (including *Lyonia*) probably have entered the Caribbean region from the west (i.e., via Mexico and western Cuba). *Lyonia* could not easily have migrated from the north, since an oceanic barrier at least as extensive as the present one separated continental North America and the Greater Antilles in this region during the middle Tertiary (Graham & Jarzen, 1969; Graham, 1972). *Lyonia* was probably dispersed to the topographically diverse Oligocene uplands of the Caribbean by wind because the seeds are small and light and can be blown about. Long-distance dispersal events must be very rare, however, since the great majority of the seeds fall within a short distance of the parental plant (pers. obs.). Once *Lyonia* was established within the Antilles, radiation occurred into diverse habitats, the taxa being primarily isolated by geographic, ecological, and genetic barriers (see below). *Lyonia* possibly spread throughout the Greater Antilles when this region still existed as a single (or two?) large land mass(es), or when the water barriers separating the islands were not as extensive as they are today. The species of Cuba, when compared to those of Puerto Rico, Hispaniola, and the Virgin Islands, are quite distinct, suggesting that Cuba may early have become separate (or perhaps was always distinct) from these islands. *Lyonia rubiginosa* var. *stahlii,* which now exists only on a few of the highest peaks of the Puerto Rican Cordillera Central, and *L. rubiginosa* var. *rubiginosa,* which exists (or once existed) in a population of only a few individuals atop a single peak on St. Thomas, probably are relicts that were more widespread when higher elevations existed on these islands during the Oligocene and Miocene.

As was shown above, within the genus *Lyonia,* the species growing on each island are nearly always most closely related to others on the same island. The generalized species of each island tend to be similar morphologically and anatomically, and they usually occur in mesic to slightly xeric habitats, such as cloud forests, moist montane forests, or low-elevation pine forests. The advanced species of each of the islands are very distinctive and are usually adapted to various more rigorous habitats, such as thickets on red lateritic soils rich in iron oxide and often developed over serpentine (e.g., *Lyonia glandulosa, L. macrophylla, L. nipensis, L. obtusa, L. truncata* var. *truncata*); sterile, white-sand savannas (e.g., *L. ekmanii, L. myrtilloides*); high-elevation pine forests on igneous soils (e.g., *L. urbaniana, L. heptamera, L. tuerckheimii, L. alpina*); or pine forests or thickets over limestone (some populations of *L. truncata* and *L. microcarpa*).

Lyonia species are rather narrowly endemic and are adapted to specific ecological situations and elevational ranges. Many taxa are found only in single mountain ranges (see TABLES 4 and 5), and a few, such as *L. toaënsis* and *L. rubiginosa* var. *rubiginosa*, are endemic to single peaks. However, on each island a few taxa, such as *L. truncata* and *L. rubiginosa* var. *costata* on Hispaniola, or *L. macrophylla, L. affinis*, and *L. latifolia* on Cuba, are

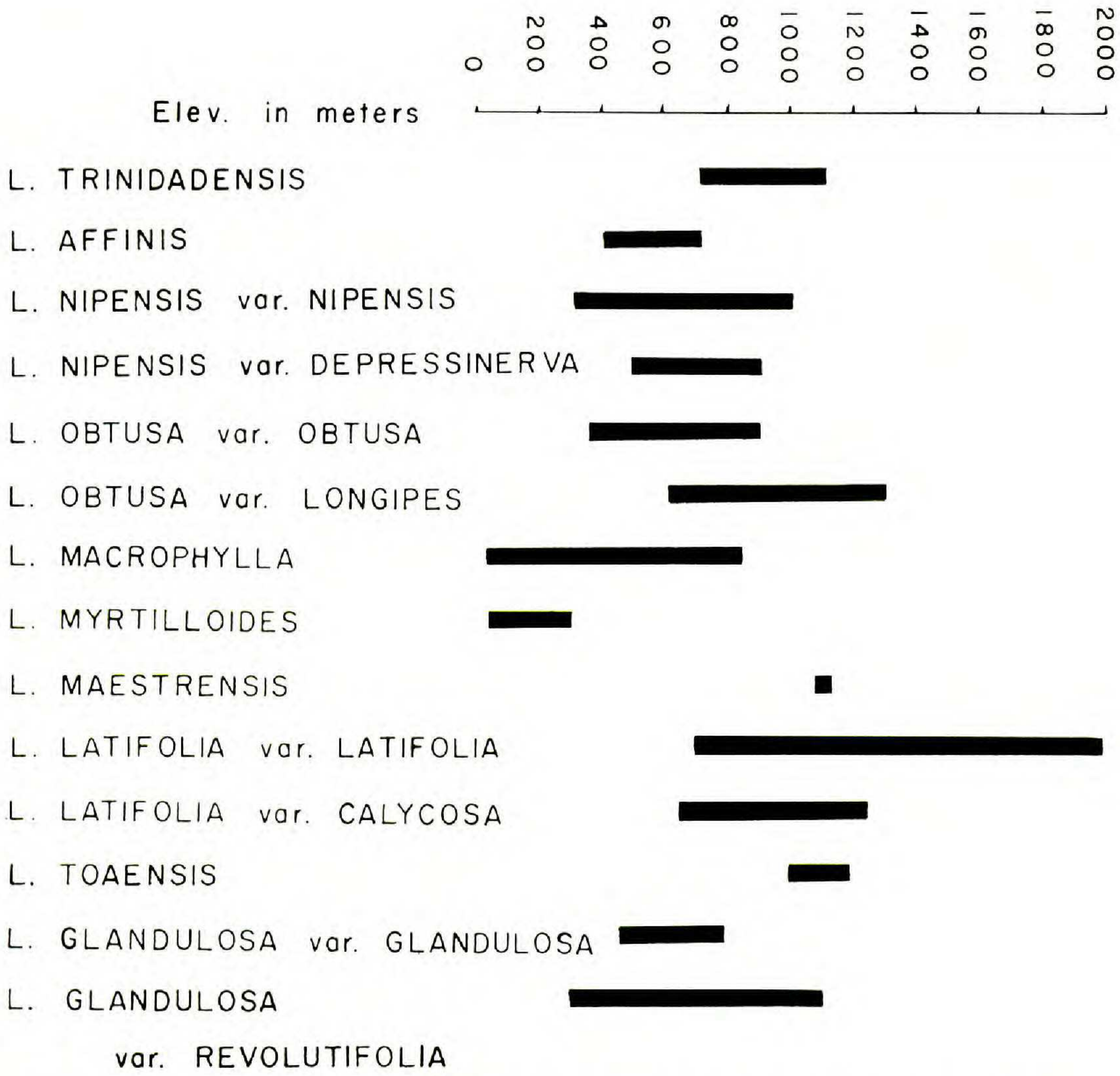


FIGURE 3. Altitudinal ranges of species and varieties of *Lyonia* sect. LYONIA in Cuba (*L. elliptica* and *L. ekmanii* not plotted because of insufficient data).

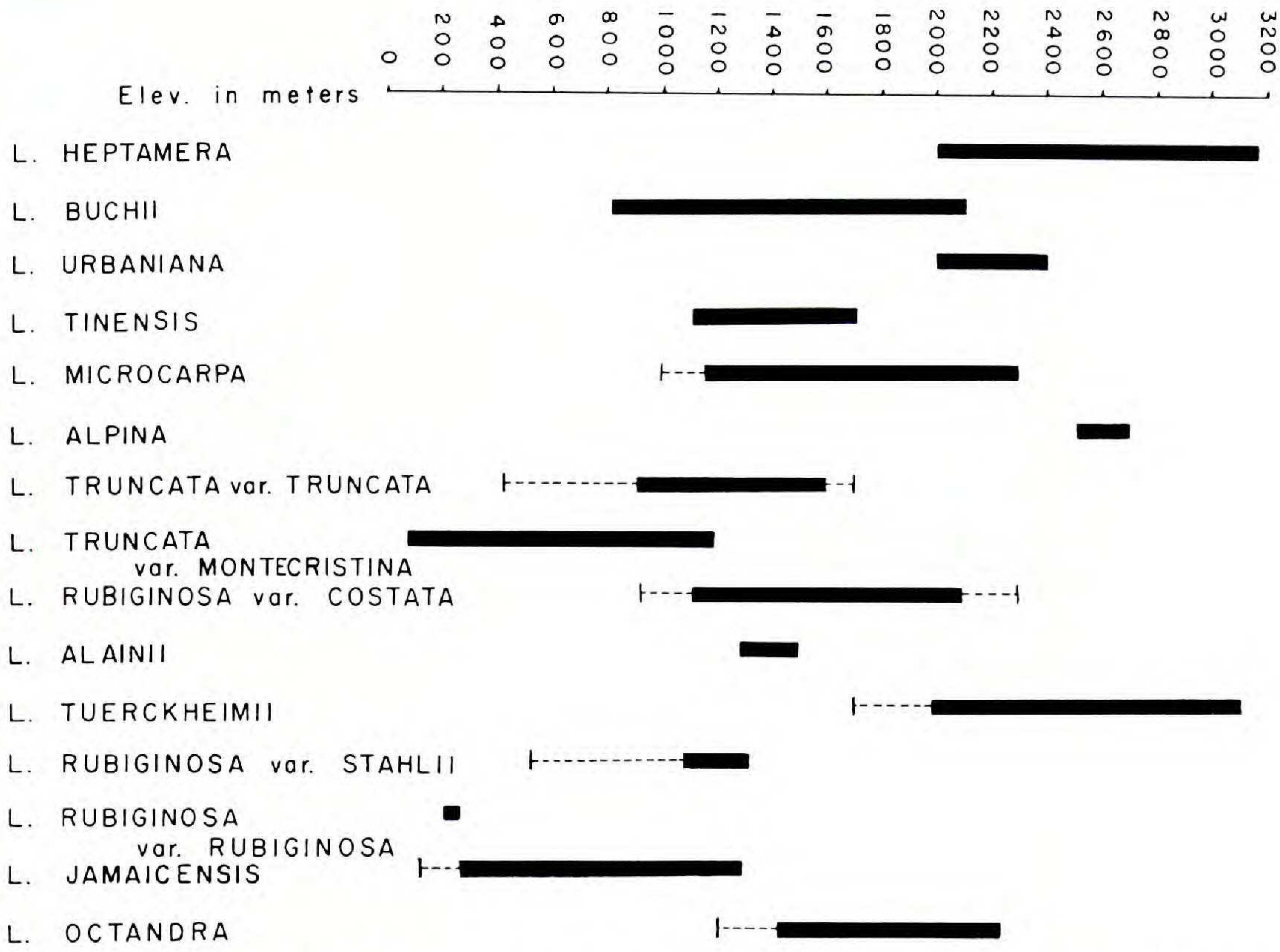
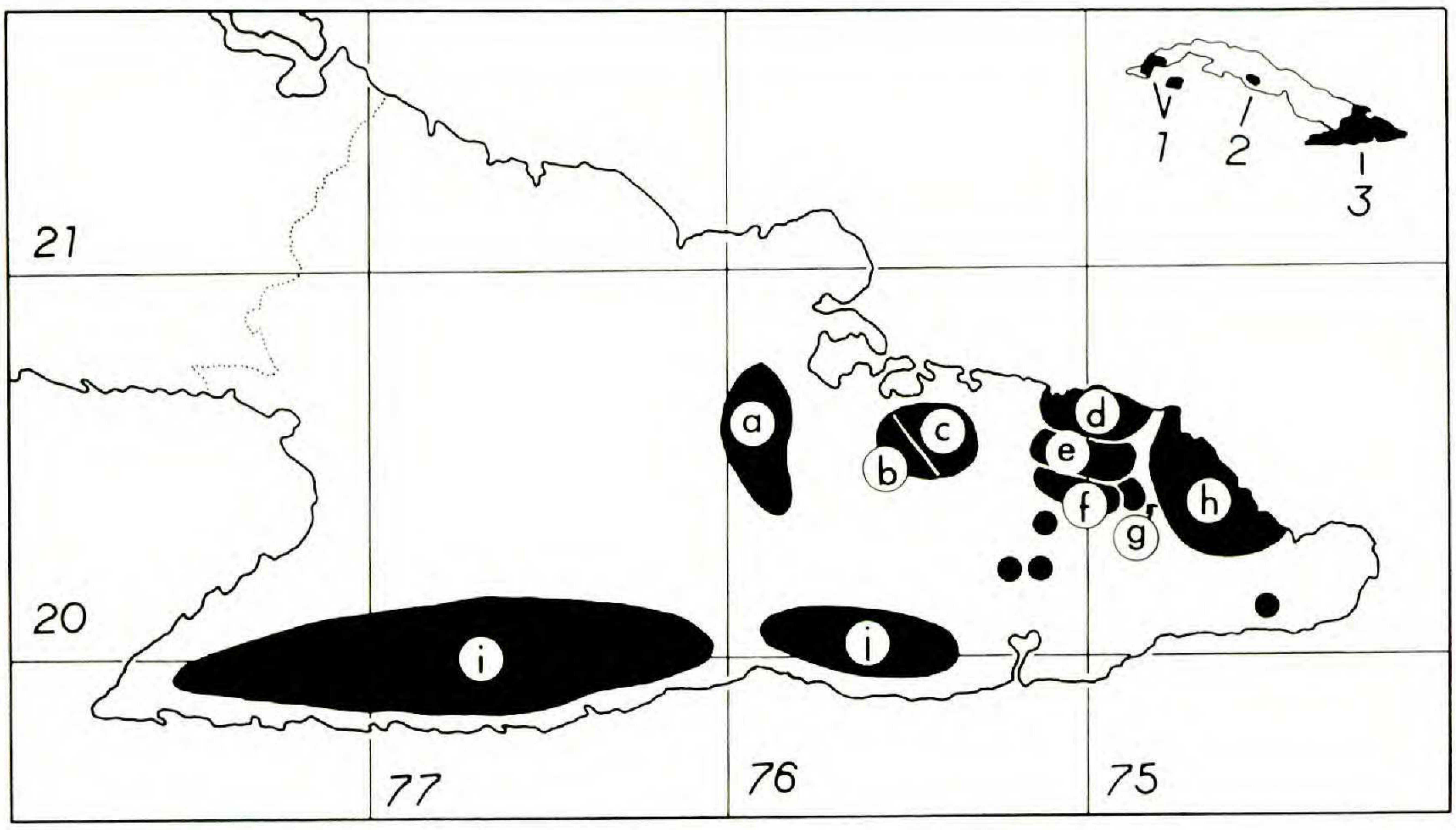


FIGURE 4. Altitudinal ranges of species and varieties of *Lyonia* sect. LYONIA in Hispaniola, Puerto Rico, St. Thomas, and Jamaica.

widespread. These species are often composed of many distinct, somewhat different populations that have sometimes been recognized by earlier botanists as separate species. The most extensive adaptive radiation has occurred in Cuba and Hispaniola, the Caribbean islands with the greatest diversity of topography, the greatest isolation of ecological niches, and the most widely varying soil types (see Howard, 1973).

When the elevational and geographic ranges of the species of Jamaica, Cuba, and Hispaniola are studied (FIGURES 3–6; MAPS 1, 2; TABLES 4, 5), several interesting patterns emerge. Hispaniola, which has the highest mountains of the Greater Antilles, has well-developed zones of vegetation, especially in the Cordillera Central and the Massif de la Selle–Sierra de Baoruco (see Ciferri, 1936), and many of the taxa of *Lyonia* on this island are isolated by elevational barriers (FIGURES 5, 6). In the Cordillera Central the mountains are covered with a low-elevation *Pinus occidentalis* forest up to ca. 2000 meters, where there is a narrow zone of cloud forest. Above this zone there develops a unique high-elevation *P. occidentalis* forest with many shrubs and herbs that do not occur in the pine forests of the lower slopes.

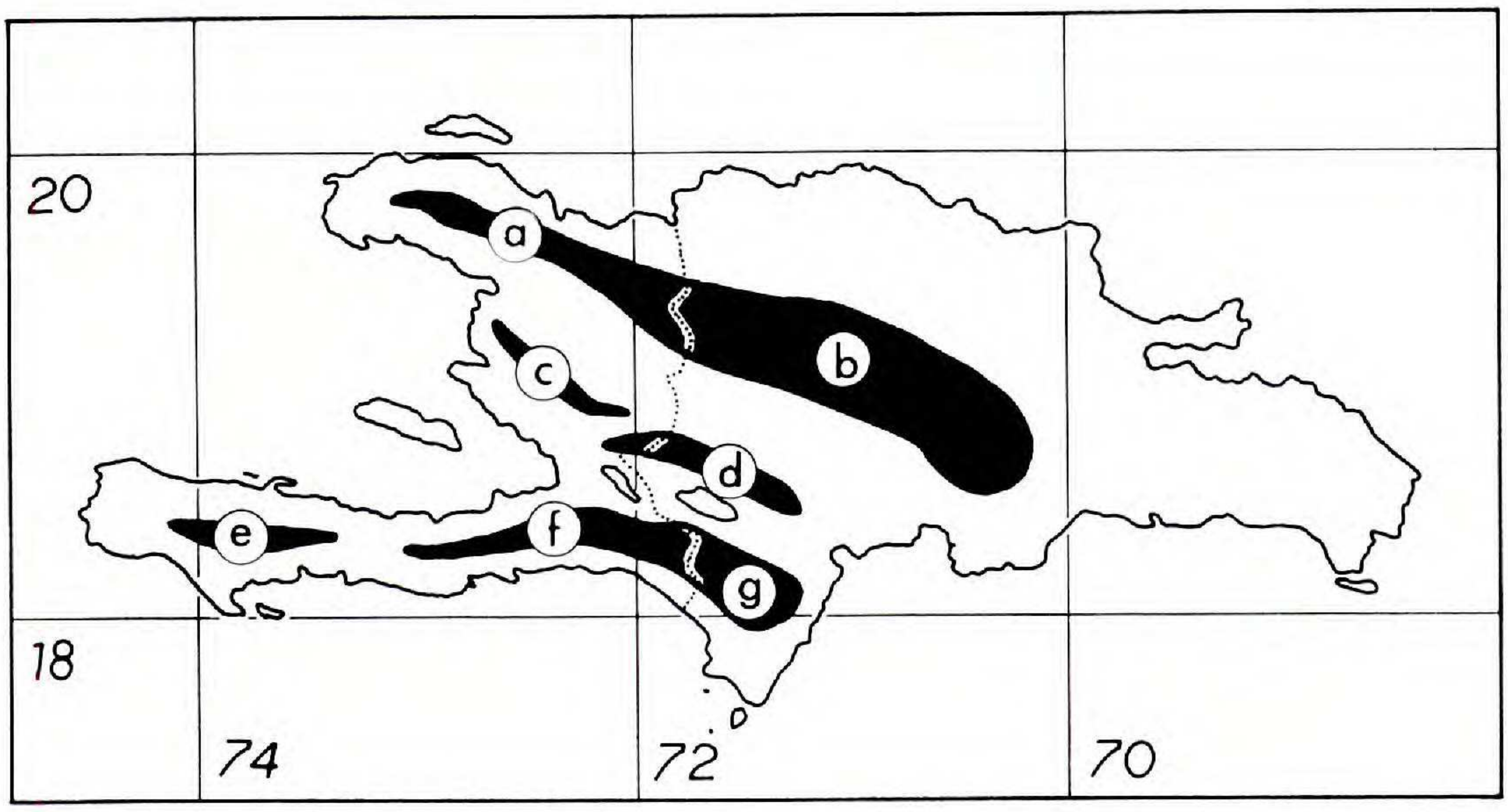
Lyonia has two major centers of endemism in Hispaniola: the Cordillera Central, where eight taxa are indigenous and five are endemic; and the Massif de la Selle–Sierra de Baoruco, with six taxa, three of which are endemic (MAP 2 and TABLE 4). These areas are also centers of diversity of other



MAP 1. Geographic areas of Cuba where *Lyonia* occurs (above, right): 1, Pinar del Río and Isla de Pinos; 2, Sierra de Trinidad and Sierra de Sancti Spiritus; 3, mountains of Oriente. Geographic areas of Oriente (below): a, Sierra de Nipe; b, Sierra de Mícara; c, Sierra de Cristal; d, Moa region; e, Sierra de Moa; f, Sierra de Toa; g, Sierra del Frijol; h, Baracoa region; i, Sierra Maestra; j, Gran Piedra.

genera (see Urban, 1923; Moscoso, 1943; Howard, 1973).

Many *Lyonia* species are isolated ecologically, with one taxon occurring at low elevations and a related one at higher altitudes. In the Cordillera Central this pattern is best illustrated by three pairs of species (see FIGURE 5): *Lyonia heptamera–L. buchii; L. tuerckheimii–L. rubiginosa* var. *costata;* and *L. urbaniana–L. tinensis.* The first-mentioned taxon of each of these three pairs characteristically occurs in the high-elevation pine forest, with the second in the isolated low-elevation pine forest. The altitudinal ranges of *L. heptamera* and *L. tuerckheimii* seem to overlap slightly with those of *L. buchii* and *L. rubiginosa* var. *costata,* respectively, since the high-elevation *Pinus occidentalis* forest begins at slightly different altitudes in various portions of the Cordillera Central due in part to edaphic factors and local wind currents. In the Massif de la Hotte, *L. rubiginosa* var. *costata* reaches elevations of ca. 2300 meters, but *L. tuerckheimii* does not occur; in the Cordillera Central, where both grow, *L. rubiginosa* reaches no higher than ca. 2100 meters. The elevational range of *L. rubiginosa* var. *costata* also appears to overlap that of *L. truncata,* a plant of dry, open pine forests, but actually these two related species do not occur together. In the Cordillera Central, *L. rubiginosa* extends only as low as ca. 1400 meters, while *L. truncata* var. *montecristina* grows as high as 1200 meters; in the Massif de la Selle, *L. rubiginosa* var. *costata* only extends as low as 1600 meters, and *L. truncata* var. *truncata* grows up to ca. 1600 meters (FIGURE 6)! *Lyonia rubiginosa* var. *costata* can be found as low as 1100 or 900 meters, but



Map 2. Geographic areas where *Lyonia* occurs in Hispaniola: a, Massif du Nord; b, Cordillera Central; c, Massif des Cahos; d, Sierra de Neiba; e, Massif de la Hotte; f, Massif de la Selle; g, Sierra de Baoruco (including Monteada Nueva).

only in localities where *L. truncata* does not occur (i.e., Monteada Nueva or a few localities in the Massif du Nord). *Lyonia alpina,* probably related to *L. truncata* var. *truncata,* grows at much higher elevations in the Massif de la Selle than does the latter taxon. Other taxa of Hispaniola (e.g., *Lyonia truncata* var. *truncata–L. truncata* var. *montecristina; L. microcarpa–L. urbaniana*) are geographically isolated by their occurrence in mountain ranges that are separated by low areas of xerophytic vegetation in which *Lyonia* cannot grow. The former taxon of each pair occurs in the Massif de la Selle–Sierra de Baoruco, and the latter in the Cordillera Central. *Lyonia alainii* is also geographically isolated from the related *L. tuerckheimii* and *L. rubiginosa* var. *costata.*

The two Jamaican species, *Lyonia jamaicensis* and *L. octandra,* are also elevationally isolated, with *L. octandra* occurring in the elfin or cloud forests at the summits of the Blue Mountains and *L. jamaicensis* growing in the lower dry-slope forests (Figure 4).

In contrast to the taxa of Hispaniola and Jamaica, which have widely diverse elevational ranges, the taxa of Cuba (Figure 3), with a few exceptions, are rather uniform with respect to altitudinal distribution. Cuba is a large island with many semi-isolated mountain ranges (Map 1), but these tend to be lower in elevation than those of Hispaniola.

In Cuba most of the taxa are limited to either Oriente or Pinar del Río, although one species (*Lyonia trinidadensis*) occurs in the mountains of Las Villas Province, near the center of the island. *Lyonia* is especially diverse in the mountains of Oriente, an area that is also the center of diversity for many other genera (see Seifriz, 1943; León, 1946; León & Alain, 1957; Alain, 1953, 1958; Howard, 1973). In Oriente, the Sierra de Cristal, Sierra

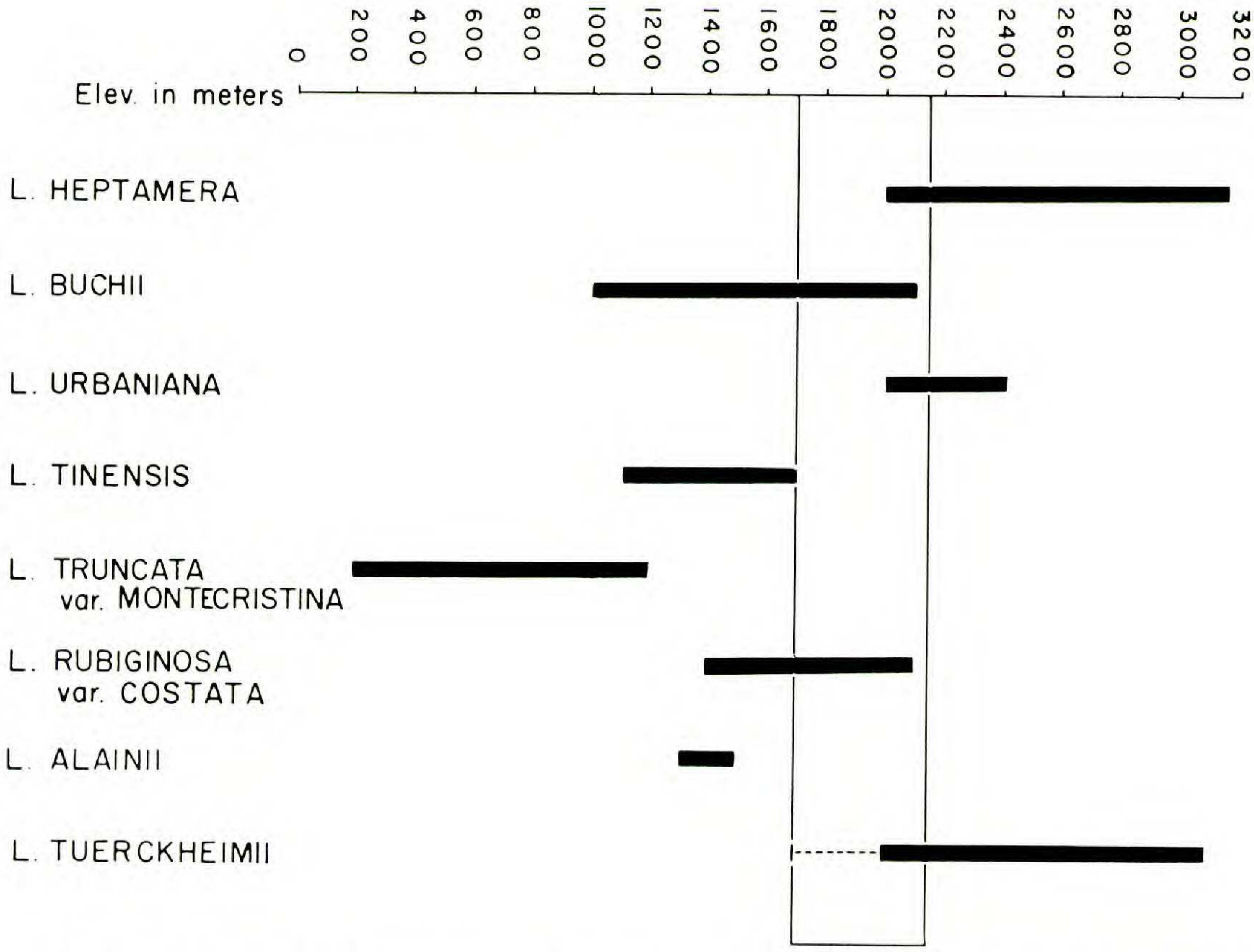


FIGURE 5. Altitudinal ranges of species and varieties of *Lyonia* occurring in Cordillera Central of Hispaniola. Vertical rectangle between ca. 1700 and 2150 m. indicates zone of cloud forests; forests dominated by *Pinus occidentalis* occur above and below this zone.

Maestra, Sierra de Nipe, Moa plateau, Sierra de Moa, Sierra de Toa, and Baracoa region show the greatest diversity in species of *Lyonia,* and most of these areas have at least one endemic taxon (MAP 1 and TABLE 5). This high degree of endemism in the various mountain ranges of Oriente was early noticed by E. L. Ekman, who collected extensively in Cuba and Hispaniola.

Because of the rather low elevation of many of these mountain ranges, there is less altitudinal variation and the species tend to be separated geographically. The geographically isolated areas of high endemism are often localities with unusual ecological conditions: for example, the *Pinus cubensis* forests and thickets on the red lateritic soils of such areas as Moa, Baracoa, and the Sierra de Nipe (overlying serpentine; see also Iturralde, 1976); the white-sand savannas of Pinar del Río; or the cloud forests, high-elevation thickets, or pine forests of the Sierra Maestra. Some geographically isolated Cuban taxa include *Lyonia nipensis* var. *nipensis*-var. *depressinerva; L. obtusa* var. *obtusa*-var. *longipes; L. latifolia* var. *latifolia*-var. *calycosa; L. elliptica-L. affinis; L. macrophylla-L. ekmanii; L. glandulosa* var. *glandulosa*-var. *revolutifolia* (both isolated from *L. toaënsis*). A few species, such as *L. affinis* and *L. latifolia* of the Sierra Maestra, may also be altitudinally isolated.

A few species of *Lyonia* (all of North America or eastern Asia) have very wide geographic and/or altitudinal ranges and are adapted to a wide range of ecological conditions. These species include *L. mariana, L. lucida, L. ligustrina, L. villosa,* and *L. ovalifolia* (FIGURE 7). It is interesting that in sect. LYONIA there has been extensive speciation within the topographically and ecologically diverse West Indian islands, while in sect. PIERIDOPSIS there has not been similar speciation in the equally or even more diverse mountains of eastern Asia. The magnitude of morphological variation within the two groups is roughly similar, but in sect. LYONIA the variation is discontinuous, thus allowing the recognition of many species, while in sect. PIERIDOPSIS it tends to be continuous, allowing—at most—the recognition of intergrading geographic varieties. This difference in pattern of variation is possibly the result of genetic or historico-climatic differences between these two groups.

Within eastern Asia, the greatest diversity is reached in Yunnan Province, China, and adjacent regions (MAP 3), where the most primitive species (*Lyonia compta* and *L. chapaënsis*) also occur. The distribution of *Lyonia* sect. PIERIDOPSIS illustrates the classic Sino-Japanese distribution pattern shown by many mesophytic temperate genera. Hara (1966) has listed 128 examples of taxa showing this pattern, including the ericaceous genera *Monotropa* L., *Monotropastrum* H. Andres, *Enkianthus* Lour., *Lyonia,* and *Pieris.* Some species occurring throughout the full range from Japan to the Himalayas show little variation, but most either vary infraspecifically over that area (e.g., *L. ovalifolia*) or have closely related species in Japan and the Himalayas.

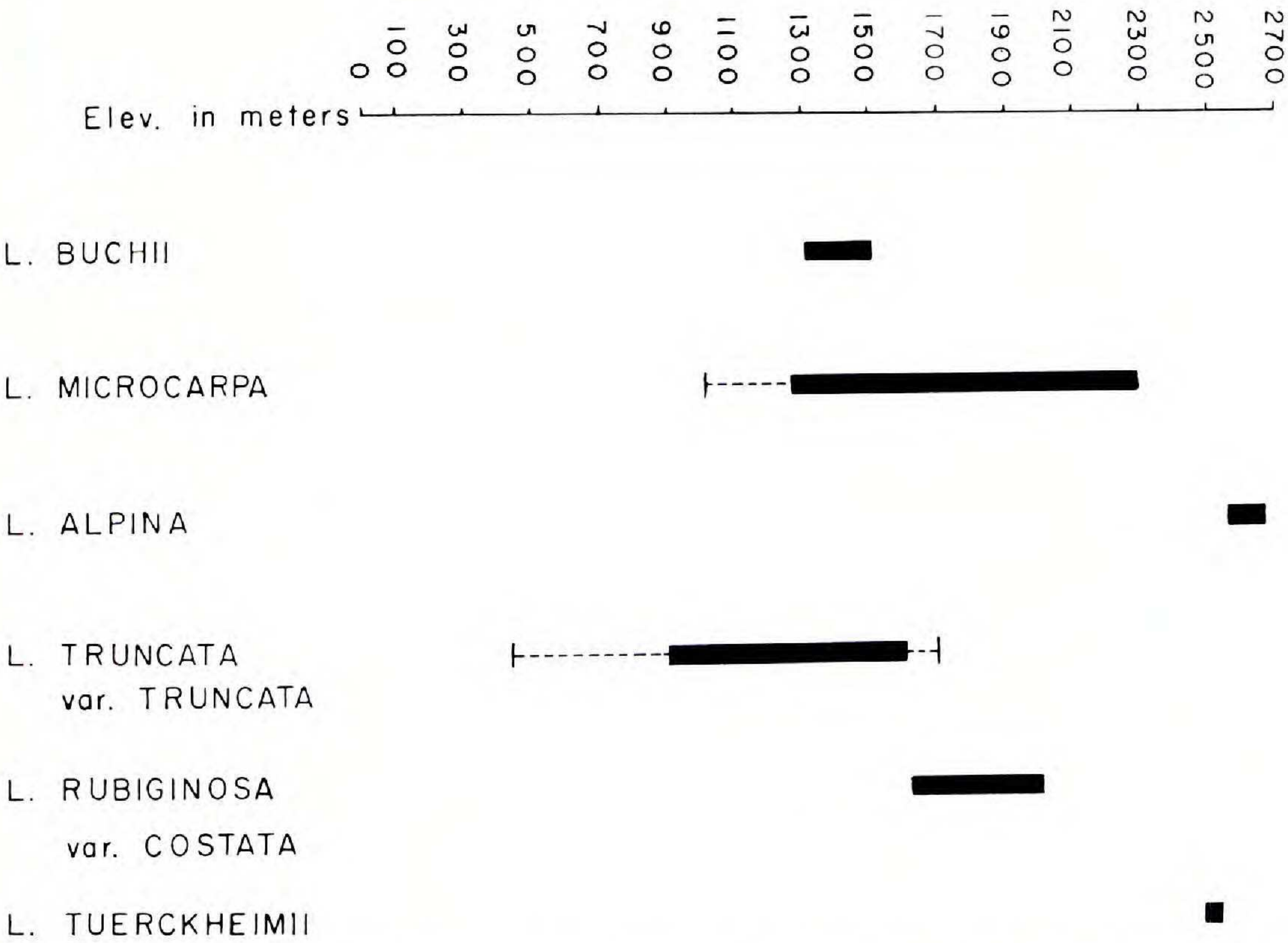


FIGURE 6. Altitudinal ranges of species and varieties of *Lyonia* occurring in Massif de la Selle–Sierra de Baoruco, Hispaniola.

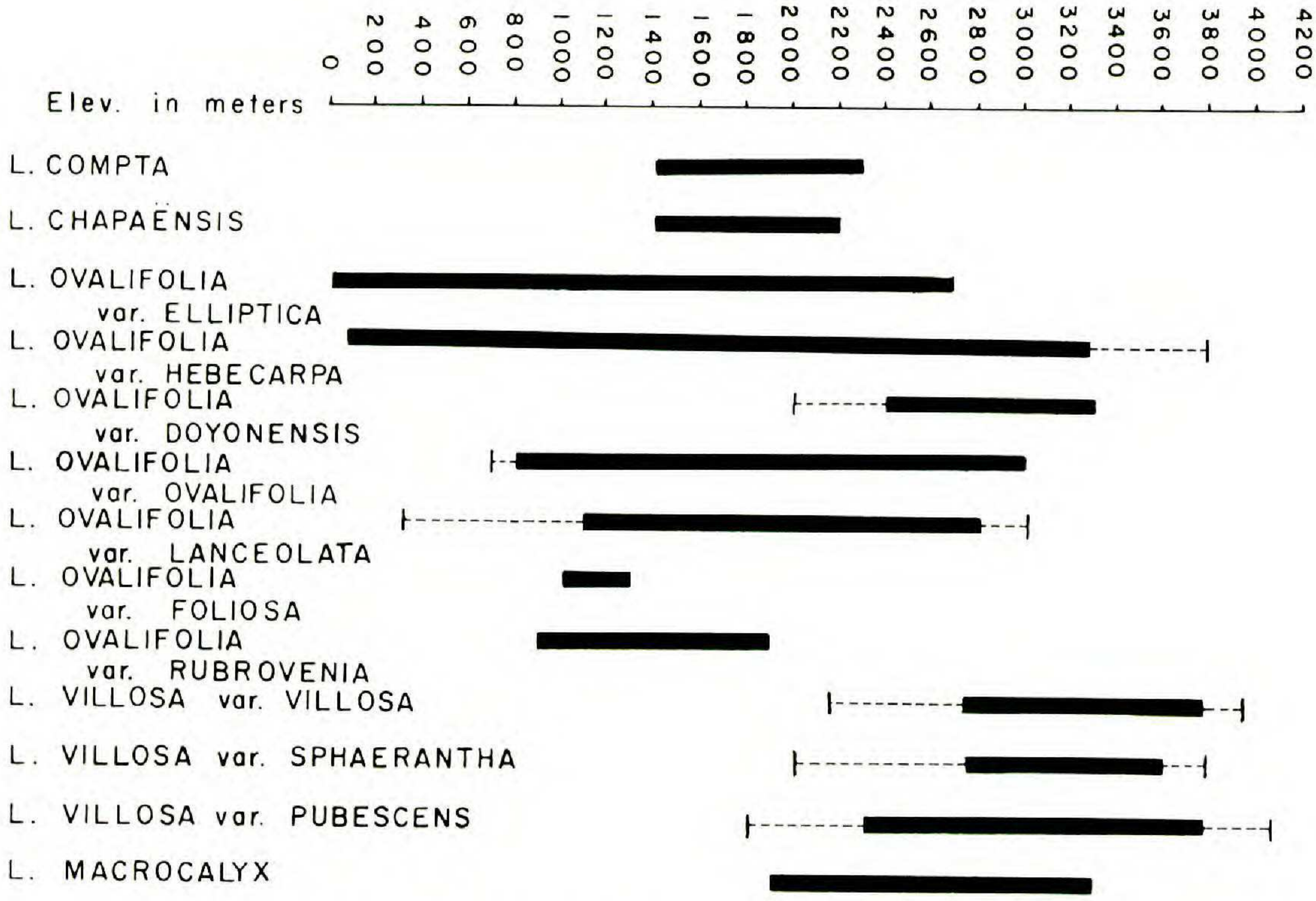
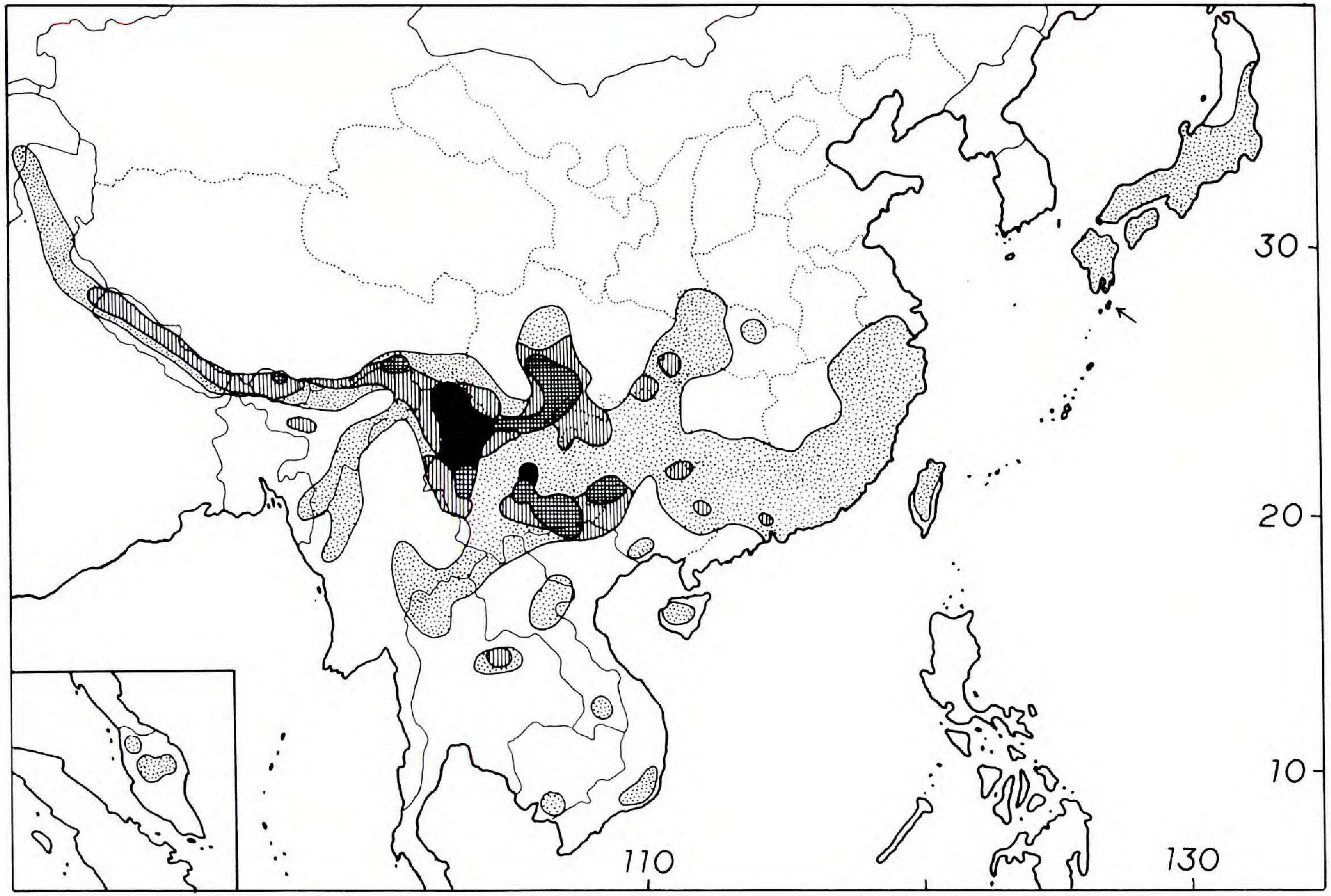


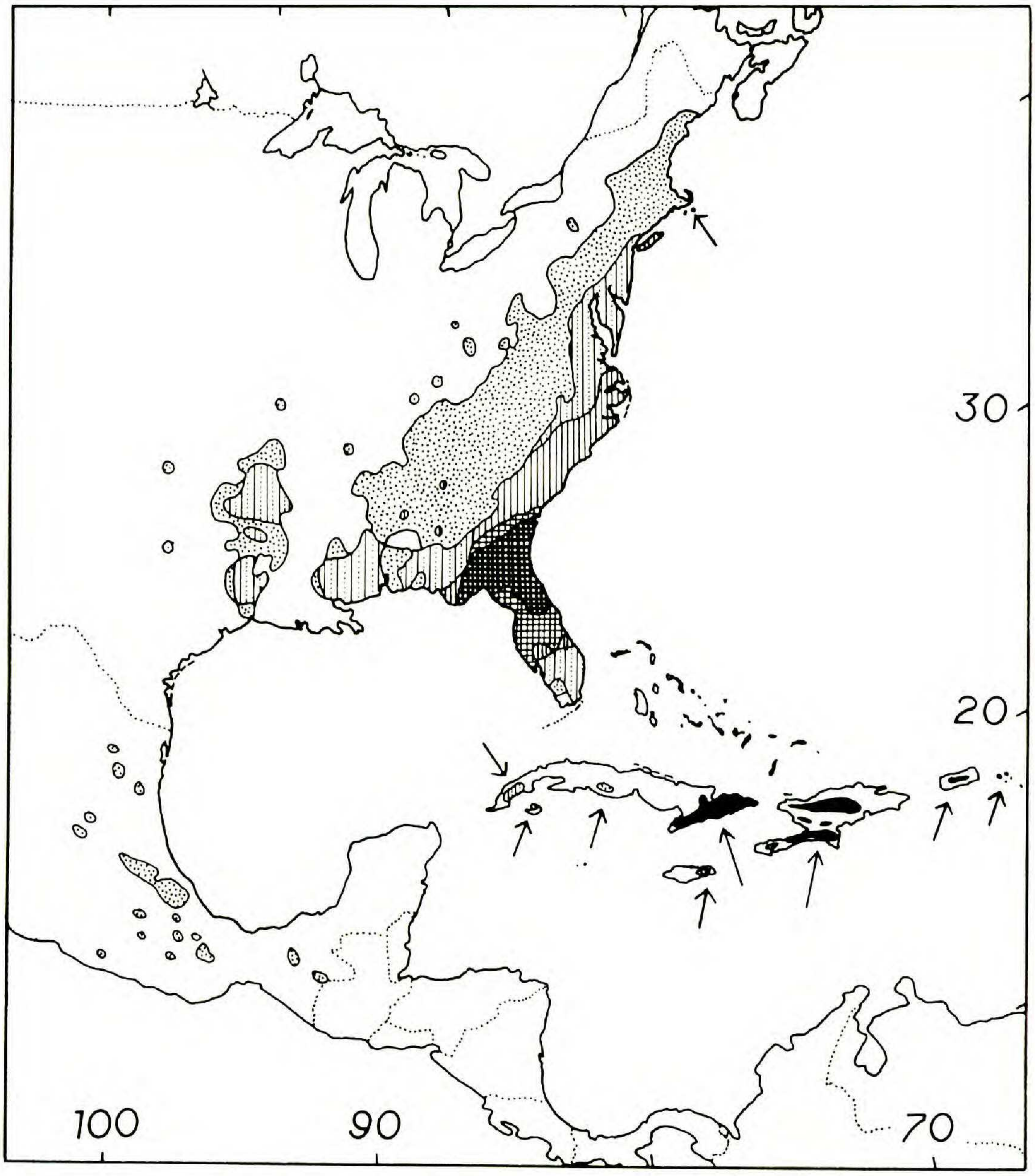
FIGURE 7. Altitudinal ranges of taxa of *Lyonia* sect. PIERIDOPSIS.

The center of diversity of many of these genera is found in Yunnan, and many also occur in North America. The morphological variation within *L. ovalifolia* is greatest in Yunnan, where four varieties are found; the varieties tend to be altitudinally and/or ecologically isolated. *Lyonia villosa*, a species closely related to *L. ovalifolia*, occurs only from the western Himalayas to Szechwan and Yunnan and usually grows at higher elevations than does *L. ovalifolia* (FIGURE 7).

In continental North America, the greatest number of *Lyonia* species is found in northern Florida, southeastern Georgia, and southern South Carolina, where *L. mariana, L. lucida, L. ligustrina, L. ferruginea,* and *L. fruticosa* all occur (MAP 4). These species are all clearly demarked and can often be found growing nearly side by side, although *L. lucida* is usually in wetter sites than *L. mariana*, and *L. ferruginea* tends to grow in more shaded and/or well-drained areas than *L. fruticosa*. It is probable that the geographic range of *Lyonia* in continental North America has not always been as it is today. There is now considerable evidence that significant vegetational displacement took place during times of glacial advance (Frey, 1953; Whitehead & Barghoorn, 1962; Watts, 1970; Whitehead, 1972; Davis, 1976). The full glacial pollen assemblages in these studies conducted in the southern United States are often quite different from modern pollen assemblages of the same region. Whitehead (1972), in his study of the environmental history of the Dismal Swamp, states that *Taxodium-Nyssa* forests have only characterized the swamp for the past 3500 years; before that time, the region was occupied by more northern forest types. *Lyonia lucida* and *L. ligustrina* var. *foliosiflora*, which



MAP 3. Generalized distribution of *Lyonia* sect. PIERIDOPSIS, showing center of diversity in Yunnan, China. Pattern indicates number of taxa present: stipples, 1; vertical lines, 2; cross hatching, 3; solid black, 4 to 7.



MAP 4. Generalized distribution of *Lyonia* sects. LYONIA, MARIA, and ARSENOCOCCUS, showing centers of diversity in Greater Antilles and southeastern United States. Pattern indicates number of taxa present: stipples, 1; vertical dotted and solid lines, 2; vertical solid lines, 3; light cross hatching, 4; heavy cross hatching, 5; solid black, 6 to 10.

today reach their northernmost point in the Dismal Swamp, have likely rather recently migrated into this region from the south. Disjunct populations of *L. lucida* are found around several ponds in Bartow Co., Georgia, northwest of Atlanta. Watts (1970) found that familiar southern tree genera such as *Liquidambar* and *Nyssa*, and Coastal Plain species such as *Itea virginica* and *Psilocarya nitens*, migrated into the vicinity of these ponds in postglacial times. It is likely that *L. lucida, L. mariana,* and *L. ligustrina* have all moved northward following the Wisconsin Ice recession. *Lyonia ligustrina* var. *ligustrina* is most diverse in the southern Appalachians but extends northward to southern Maine; *L. mariana* seems to have followed the Coastal Plain northward as far as southeastern Connecticut and Long Island, New York. Braun (1947), however, felt that major changes of vegetation were limited to the Coastal Plain, with the floral composition of the Appalachian highlands having been only slightly affected, and Graham (1973, p. 304) states that "a conservative view of vegetational history in the southeast would be a community definitely influenced by fluctuating Pleistocene environments . . . but . . . still retaining the general aspect and composition of the deciduous forest in a regional sense." It is likely that there was some mixing of northern and southern taxa during the Pleistocene.

No species of *Lyonia* occurs in the Mississippi embayment region, and *L. mariana* occurs disjunctly in the Atlantic Coastal Plain and in eastern Texas, Arkansas, and several neighboring states. There are a number of plants that show similar dichotomous distributions; some are listed by Duke (1961) and by Gillis (1971).

ECOLOGY

The genus occurs in a wide variety of habitats, but characteristically prefers acid soils (pH sometimes as low as 2.8, as in *Lyonia octandra;* Tanner, 1977). Only rarely do species occur over limestone, but *L. truncata* and *L. microcarpa* have been seen growing in the lateritic soil filling the cracks of eroded limestone rocks, and *L. rubiginosa* var. *costata* growing on organic soil developed over a limestone bedrock (pers. obs.). Many Cuban species (e.g., *L. nipensis, L. obtusa, L. glandulosa, L. macrophylla*) occur on red lateritic soils developed by the weathering of underlying serpentine rocks. Other species, such as *L. heptamera, L. urbaniana, L. tinensis, L. tuerckheimii,* and *L. rubiginosa,* of the Cordillera Central (Hispaniola), grow on soils derived from igneous rocks. Most of the species of the southeastern United States and of western Cuba occur on siliceous soils. Species such as *L. mariana, L. ligustrina,* and *L. lucida* also grow in highly organic soils such as those of bogs and swamps. Several Caribbean taxa (especially those of cloud forests, such as *L. octandra* and *L. rubiginosa*) can also be found in organic soils.

The Caribbean species occur in moist montane or cloud forests, high- or low-elevation pine forests, savannas, or thickets. They range in altitude from nearly sea level to 3175 meters. Thus, *Lyonia heptamera* can be found at the top of the highest peak of Hispaniola (Pico Duarte, 3175 meters), while *L. myrtilloides* and *L. lucida* grow near sea level in Pinar del Río, Cuba, and *L. macrophylla* occurs just above sea level near Moa, Cuba. The region around Moa, because of its lateritic soil, has many normally montane species growing just above sea level. In Hispaniola *L. truncata* var. *montecristina* has been collected from elevations as low as 100 meters (FIGURE 4).

The continental North American and eastern Asian species of *Lyonia* are often found in a wide range of habitats. *Lyonia ovalifolia,* for example, occurs in subtropical *Castanopsis* forests; warm-temperate forests of *Pinus* and/or *Quercus;* cold-temperate forests of *Tsuga, Abies,* or *Picea;* dry *Rhododendron* thickets; mixed deciduous forests; or dwarf cloud forests. *Lyonia ligustrina* also occurs in diverse ecological situations, such as moist *Taxodium* swamps, shrub bogs, *Pinus* and/or *Quercus* woods, grassy balds, thickets, and acid bogs and swamps. Both species can be found in dry, rocky situations or just above the standing water of bogs or swamps, and both often occur in ecotones such as the edge of a forest, or the margin of a pond or a swamp.

Species of *Lyonia* sprout readily after cutting or fire since they are very tolerant of disturbance. Several species (e.g., *L. fruticosa, L. mariana,* and *L. ovalifolia*) often seem to respond favorably to fires, and most taxa react positively to at least slight disturbance because they are light-loving plants and become more abundant when the overstory trees are cut. In addition, the taxa, except for those of the Greater Antilles, have the ability to spread vegetatively by underground rhizomes. Undisturbed habitats within the Caribbean and in Mexico are fast disappearing, and it is thus fortunate that most species of *Lyonia* are only little harmed by slight human disturbance. Shrubs of *L. buchii, L. rubiginosa,* and *L. truncata* grow in the Dominican Republic along roadsides where the surrounding vegetation is cut and heavily grazed, and *L. truncata* also occurs on reclaimed aluminum mine areas near Aceitillar (pers. obs.); if the disturbance is strong enough, however, even *Lyonia* will be eliminated.

As the human population of these areas increases, one has to go higher and higher into the mountains to reach undisturbed and floristically diverse habitats, and the danger of extinction, especially for narrowly endemic or uncommon taxa, is increasing dramatically. *Lyonia rubiginosa* var. *rubiginosa,* which is endemic to the island of St. Thomas, may already be extinct, since it was last collected in 1887; attempts to relocate it in 1975 were unsuccessful. Other rare or endangered taxa are *L. rubiginosa* var. *stahlii* (Puerto Rico), *L. alpina* (Haiti), *L. alainii* (Dominican Republic), *L. toaënsis* (Cuba), *L. maestrensis* (Cuba), *L. elliptica* (Cuba), and *L. ekmanii* (Cuba).

TAXONOMIC CRITERIA

Systematic relationships within the Andromedeae have often been obscured by the inconsistent use of characters, the emphasis on certain "key" characters, the use of characters that are so variable that only little taxonomic value can be assigned to them, and the neglect of many useful morphological and anatomical features. In this study, as many characters as possible from all parts of the plant have been employed, and inter- and intraspecific variation have been carefully determined.

Usually no single character can be employed throughout the genus, so different species are separated by different sets of characters. Morphological entities that show a consistent complex of character states (i.e., have no major internal discontinuities) and that are separated from other similar entities by a consistent morphological gap are considered to be species. They have definite geographic distributions and ecological preferences and are often rather uniform in flower and/or fruit morphology. Species are isolated by differences in their ecological and/or altitudinal characteristics, geographic distribution, flowering time, and floral morphology and/or genetic composition. The term "variety" has been used for the morphologically distinctive subunits comprising widespread and often ecologically variable species (see Fernald, 1940; Fosberg, 1942; Weatherby, 1942; but also Clausen, 1941). These varieties are more or less geographically and/or ecologically isolated but intergrade where they come into contact and are probably completely interfertile. Varieties have slight morphological gaps between them, tending to differ in habit, leaf morphology, indumentum, or slight anatomical peculiarities. Any two varieties of a species are usually more similar in absolute number of characters than any two species within that section. The varieties of a few Caribbean species do not naturally come into geographic contact, and thus the taxonomic rank of these entities is somewhat arbitrary. If, however, two allopatric Caribbean taxa differ from each other in only a few vegetative characters, with only a very slight morphological gap between them, they have here been treated as varieties of a single, more variable species.

The taxonomic usefulness of (and the variation within) the various characters used in this monograph are discussed below.

HABIT

The species of *Lyonia* vary from small, prostrate to erect shrubs to moderate-sized trees up to 18 meters tall. *Lyonia mariana* is distinctive in that it is a very small, erect shrub that never exceeds 1.5 meters in height. Taxa growing at high altitudes are often dwarfed (e.g., *L. villosa* often forms low (0.5–1.5 meters) thickets at high elevations in the Himalayas, and *L. alpina* only reaches ca. 0.5 meters on the highest peaks of the Massif de la Selle in Haiti). The genus is almost exclusively terrestrial, but occasional individuals of *L. octandra* have been seen growing as epiphytes on trees in moist montane forests (pers. obs.). Although the habit of many species is extremely variable, it may be consistent; thus, for example, *L. buchii* can be distinguished from *L. heptamera*, *L. ferruginea* from *L. fruticosa*, and *L. rubiginosa* from *L. tuerckheimii*, because the first of each of these pairs is characteristically arborescent and the second a low to erect shrub. The branching pattern (including internode length, density of branching, and orientation of branchlets), although variable, is also useful and helps in distinguishing the varieties of *L. truncata* from each other, *L. ferruginea* from *L. fruticosa*, and *L. urbaniana* from *L. microcarpa*.

The twigs vary from slender to very stout, from round to strongly angled, and from nearly glabrous to densely pubescent. Most species of sect. LYONIA have at least moderately ridged twigs, but *Lyonia mariana*, *L. ligustrina*, and the Asian species often have round or only very slightly angled branches, and *L. lucida* is unusual in having strongly 3-angled stems. The stoutness of the twigs is a useful character in separating *L. tuerckheimii* and *L. rubiginosa* var. *costata* but varies infraspecifically in some species, such as *L. heptamera* and *L. buchii*.

The bark is always longitudinally furrowed and is sometimes shredded; it varies in color from gray to reddish brown. It is occasionally taxonomically useful, as in distinguishing *Lyonia jamaicensis* from *L. octandra,* and *L. heptamera* from older individuals of *L. buchii.* There is much variation in the density and prominence of the vertical furrows.

Species such as *Lyonia heptamera, L. tuerckheimii, L. truncata,* and possibly

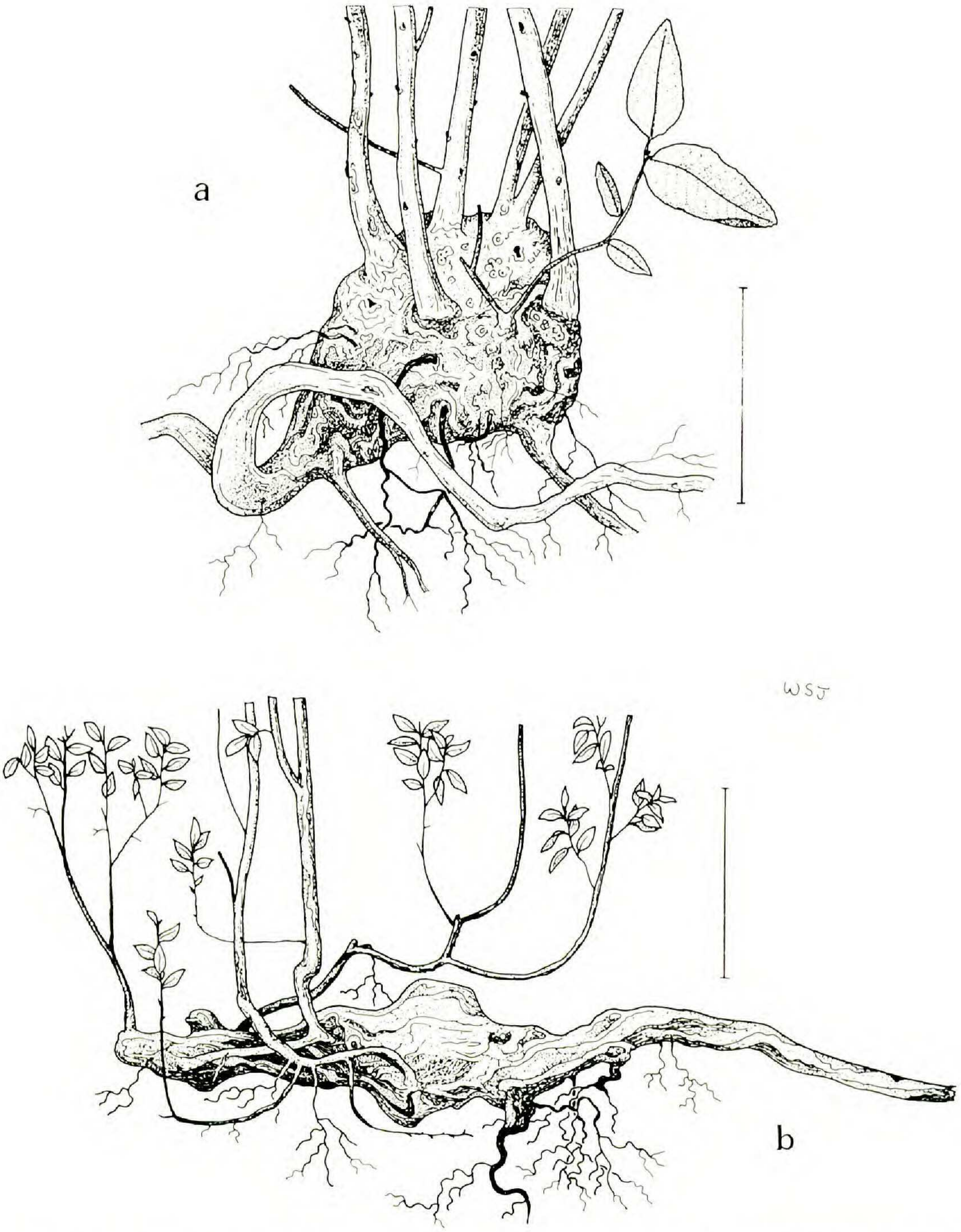


FIGURE 8. Roots and burls: a, *Lyonia heptamera,* woody underground burl (scale = 4 cm.); b, *L. ferruginea,* elongated woody burl producing underground rhizomes (scale = 10 cm.).

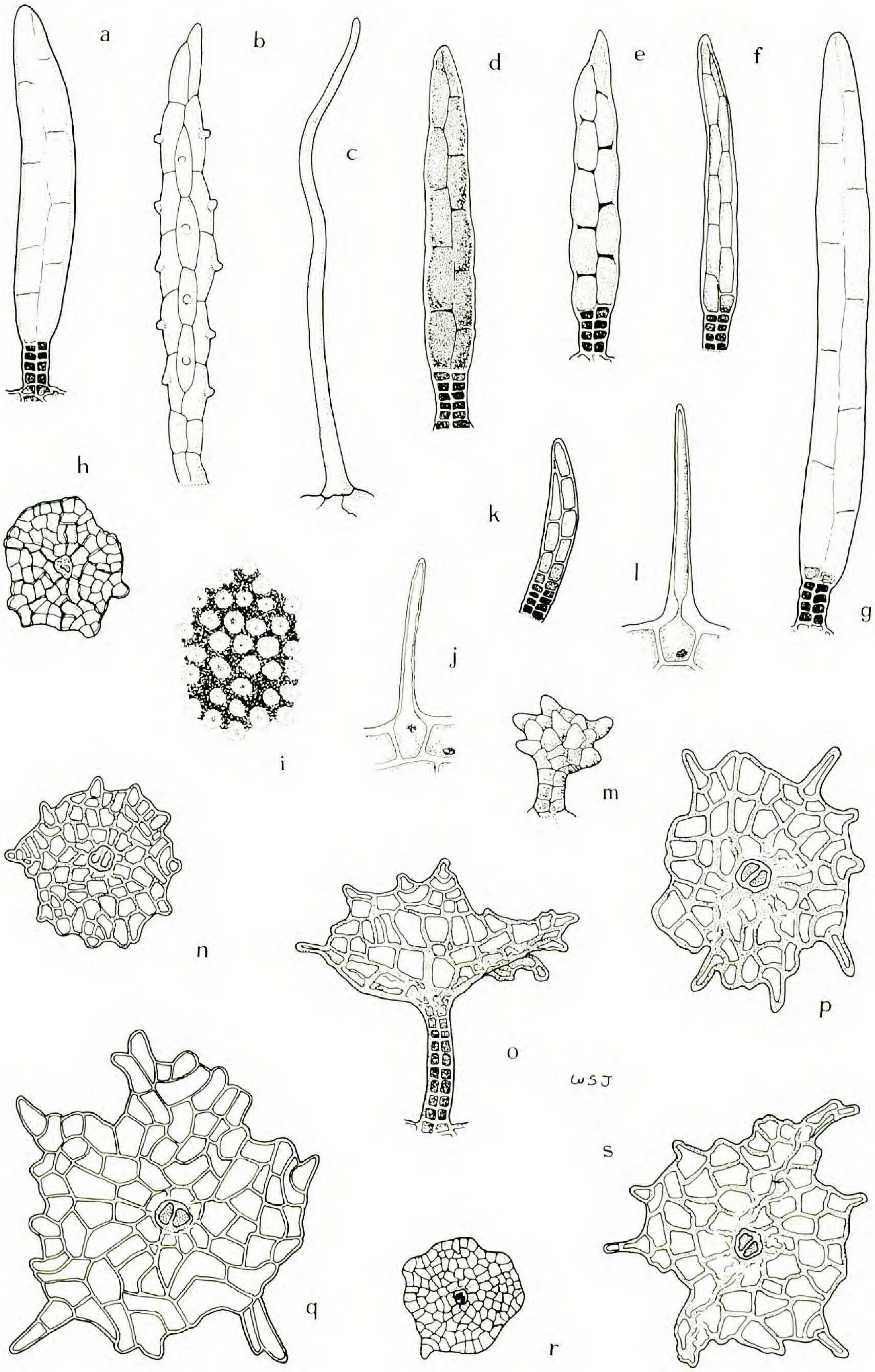
L. urbaniana frequently produce rounded, woody burls just below the soil surface (FIGURE 8). These burls are often the source of young shoots, especially when the plant is cut or is damaged by fire, and are commonly developed even in very young plants. *Lyonia ferruginea, L. fruticosa,* and *L. squamulosa* produce large, elongated burls (to ca. 10 dm.), which form both erect shoots and horizontal underground rhizomes (FIGURE 8). This rhizome network is often especially extensive in *L. fruticosa* and *L. squamulosa,* which can form large clones. In contrast, the rhizomes of *L. ferruginea* are usually few and fairly short. These three species are the only taxa of sect. LYONIA that are known to produce rhizomes. *Lyonia ligustrina, L. lucida, L. mariana,* and probably all the Asian species also spread vegetatively by rhizomes. These rhizomes have small, scalelike leaves with small axillary buds and initially develop adventitious roots only immediately above the buds (FIGURE 11). The rhizomes can continue growth underground or can turn upward and form vertical shoots with normal photosynthetic leaves. Several species form extensive colonies by means of this vegetative reproduction.

Care must be taken when dealing with habit characters because they are often strongly influenced by environmental conditions. The potential to produce rhizomes may not be realized in all situations, and shoot orientation often varies with habitat. For example, in moist, shaded conditions *Lyonia lucida* has beautifully arching branches; in sunny, seasonally dry environments it develops rigidly ascending branches similar to those of *L. fruticosa,* which also occurs in such habitats. However, the difference between *L. fruticosa* and *L. ferruginea* (rigidly ascending vs. lax branchlets) is maintained even under uniform greenhouse conditions.

INDUMENTUM

The indumentum of *Lyonia* is of three distinct types (FIGURES 9, 10): unicellular hairs; multicellular, biseriate-stalked, swollen-headed glandular hairs or peltate scales; and papillae. Many ericaceous genera have multicellular, glandular-headed hairs, and nearly all have unicellular hairs.

The peltate scales of *Lyonia* sect. LYONIA at first glance appear to be very different from the swollen-headed hairs of sects. PIERIDOPSIS, ARSENOCOCCUS, and MARIA, but both have biseriate stalks, occur in similar positions on the plant, and have similar developmental patterns (FIGURE 9); they are probably derived from a common hair type. These two types of multicellular hairs occur essentially all over the plant—on the twigs, buds, leaves, pedicels, calyx lobes, corolla (outer surface), and ovary. The density, color, persistence, and structure of the peltate scales are often very useful taxonomic characters and help to distinguish between various West Indian species. Unfortunately, the comparable characteristics of the swollen-headed hairs are either too variable or too uniform to be useful in distinguishing taxa among the Asian and North American species. An important exception is that the multicellular swollen head of these hairs is elongate in sects. PIERIDOPSIS and ARSENOCOCCUS but short in sect. MARIA. In addition, the ovary in sect. ARSENOCOCCUS is often moderately covered with swollen-headed hairs, while the ovaries in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sect. PIERIDOPSIS usually lack such hairs. The swollen head of these multicellular hairs is often reddish in sect. MARIA but varies from greenish or clear to reddish in sects. ARSENOCOCCUS and PIERIDOPSIS.

The margin of the peltate head of the scales of sect. LYONIA varies from entire to irregular or fimbriate. The scales range in color from golden to rusty (usual condition), tan, or dark brown; in many taxa they become whitish as the leaves age. Their stalks can be elongated or rather short and can be impressed into the abaxial leaf epidermis or not. The scales on a single plant may be of one morphological type or may be dimorphic in size, persistence, or structure. On the abaxial leaf surface they vary from persistent to deciduous, but they are almost always deciduous on the adaxial surface. Scales may be absent from a given plant part (e.g., the adaxial surface of the calyx lobes) in some taxa and present on the same part in others. Finally, the density of scales on leaves, corolla, calyx lobes, and other plant parts is often taxonomically useful. When taxa are compared, it is important to look at fully developed leaves, since the young shoots are always more densely lepidote than the mature ones of the same plant. A few taxa in which the above-mentioned variations are important are discussed here; others are evident in the keys. The related species *Lyonia macrophylla* and *L. obtusa* are easily distinguished by the density of ferrugineous scales on the abaxial surface of their leaves. Although most species have only sparsely lepidote corollas and lack scales on the adaxial surface of the calyx lobes, *L. nipensis* and *L. latifolia* are distinctive in having densely lepidote corollas, and the latter is unusual in that its calyx lobes are densely lepidote on both surfaces. Some species can be easily distinguished by the color of their scales: brownish in *L. urbaniana* and *L. tinensis,* more or less orange in *L. microcarpa,* and golden in *L. latifolia.* The scales of *Lyonia nipensis* var. *depressinerva* and *L. ferruginea* are characteristically of two distinct sizes; those of their relatives (*L. nipensis* var. *nipensis* and *L. fruticosa,* respectively) are usually all large. *Lyonia obtusa* and *L. alainii* have nearly entire-margined scales, while their relatives have scales that are usually irregular- or fimbriate-margined.

The distribution of unicellular hairs is of taxonomic interest, although their morphology is usually rather invariable. These hairs, which are composed of a single, elongated cell (FIGURE 9), almost always occur singly; however,

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FIGURE 9. Unicellular and multicellular hairs and peltate scales, × 150 (all except b, f, k, and m from abaxial leaf surface): a, *Lyonia ligustrina* var. *ligustrina,* multicellular hair; b, *L. villosa* var. *pubescens,* multicellular hair from filament of *Forrest 28708* (E); c, *L. ovalifolia* var. *hebecarpa,* unicellular hair; d, *L. compta,* multicellular hair; e, *L. ovalifolia* var. *rubrovenia,* multicellular hair; f, k, *L. ligustrina* var. *ligustrina,* developing multicellular hairs; g, *L. ovalifolia* var. *hebecarpa,* multicellular hair; h, p, *L. ferruginea,* peltate scales; i, *L. macrocalyx,* papillae; j, *L. ligustrina* var. *ligustrina,* unicellular hair; l, *L. mariana,* unicellular hair; m, *L. ferruginea,* developing peltate scale; n, *L. truncata,* peltate scale; o, s, *L. heptamera,* peltate scale; q, *L. latifolia,* peltate scale; r, *L. alainii,* peltate scale.

occasional paired hairs have been seen. The presence of a dense layer of unicellular hairs on the abaxial leaf surface is characteristic of many species of sect. LYONIA, but these hairs are lacking in other species (see TABLES 7, 8). Although *Lyonia mariana, L. ligustrina,* and several Asian species have similar unicellular hairs along the veins of their lower leaf surfaces, none has this characteristic dense layer. The presence of this dense pubescence is not affected by environmental conditions, but it is slightly influenced by the age of the plant, in that seedlings and juvenile shoots tend to lack these hairs or to have only a sparse covering of them. Nearly all species of *Lyonia* have unicellular hairs on the midvein of the adaxial leaf surface; within sect. LYONIA, the Cuban species (and *L. tuerckheimii*) often have unicellular hairs on the midvein of the abaxial surface as well. Similar hairs often occur on the veins of both leaf surfaces in *L. villosa, L. ovalifolia, L. ligustrina,* and *L. mariana.* The density of unicellular hairs on the twigs is variable in most species, but in certain cases it helps to distinguish between closely related species such as *L. tuerckheimii* and *L. rubiginosa,* or *L. jamaicensis* and *L. octandra.* The density of such hairs on the bracts, bracteoles, pedicels, calyx lobes, and capsules is usually not of taxonomic importance.

The leaves of a few Asian taxa (*Lyonia macrocalyx, L. villosa,* and *L. ovalifolia* vars. *doyonensis* and *ovalifolia*) are either occasionally or always papillose. The papillae are projections of the cells of the lower leaf epidermis and sometimes also of the epidermal cells of the calyx lobes (FIGURE 9). Sometimes visible only under the high-power dissecting microscope, they are often more obvious in taxa with glaucous abaxial leaf surfaces.

BUDS

The buds of *Lyonia* are ovoid and range in length from only 1–2 mm. (in most of the Caribbean species) to ca. 12 mm. (in many Asian taxa). The buds of nearly all species have two small to large imbricate scales (which are modified leaves; FIGURE 10). In *L. mariana* and occasionally in *L. lucida,* the buds have only two visible scales when very young but soon expand to reveal additional scales; the buds are glabrous or almost so. The buds of sect. LYONIA are usually densely lepidote; those of sects. PIERIDOPSIS and ARSENOCOCCUS are glabrous to moderately covered with unicellular hairs and often have a few multicellular ones. The buds of species in the last two sections often become reddish in autumn.

LEAVES

In all species of *Lyonia,* the leaves are alternate, and the lowermost ones of the shoots are typically small and scalelike. Species such as *L. mariana, L. ligustrina, L. ovalifolia,* and *L. villosa* are deciduous, with chartaceous to coriaceous leaves that often turn reddish in autumn. The leaves of *L. compta, L. lucida,* and all species of *Lyonia* sect. LYONIA are evergreen, persisting for as long as three years, and are frequently extremely coriaceous. Petiole length, although often rather variable, is sometimes taxonomically useful. Lamina size varies dramatically within many taxa, and this variability has led to the description of many species that cannot be maintained when the total range of variation is considered. Variation is especially great in the Asian and North American species of the genus. For example, the mature leaves of *L. ovalifolia* vary from ca. 21 cm. long and 12 cm. wide to only 2.5 cm. long and 1 cm. wide. However, several taxa in sect. LYONIA (e.g., *L. urbaniana, L. microcarpa*) consistently have leaves only up to 3 or 4 cm. long.

The shape of the leaf, especially of the apex, also varies greatly, sometimes within single populations or even on an individual plant. Many Caribbean

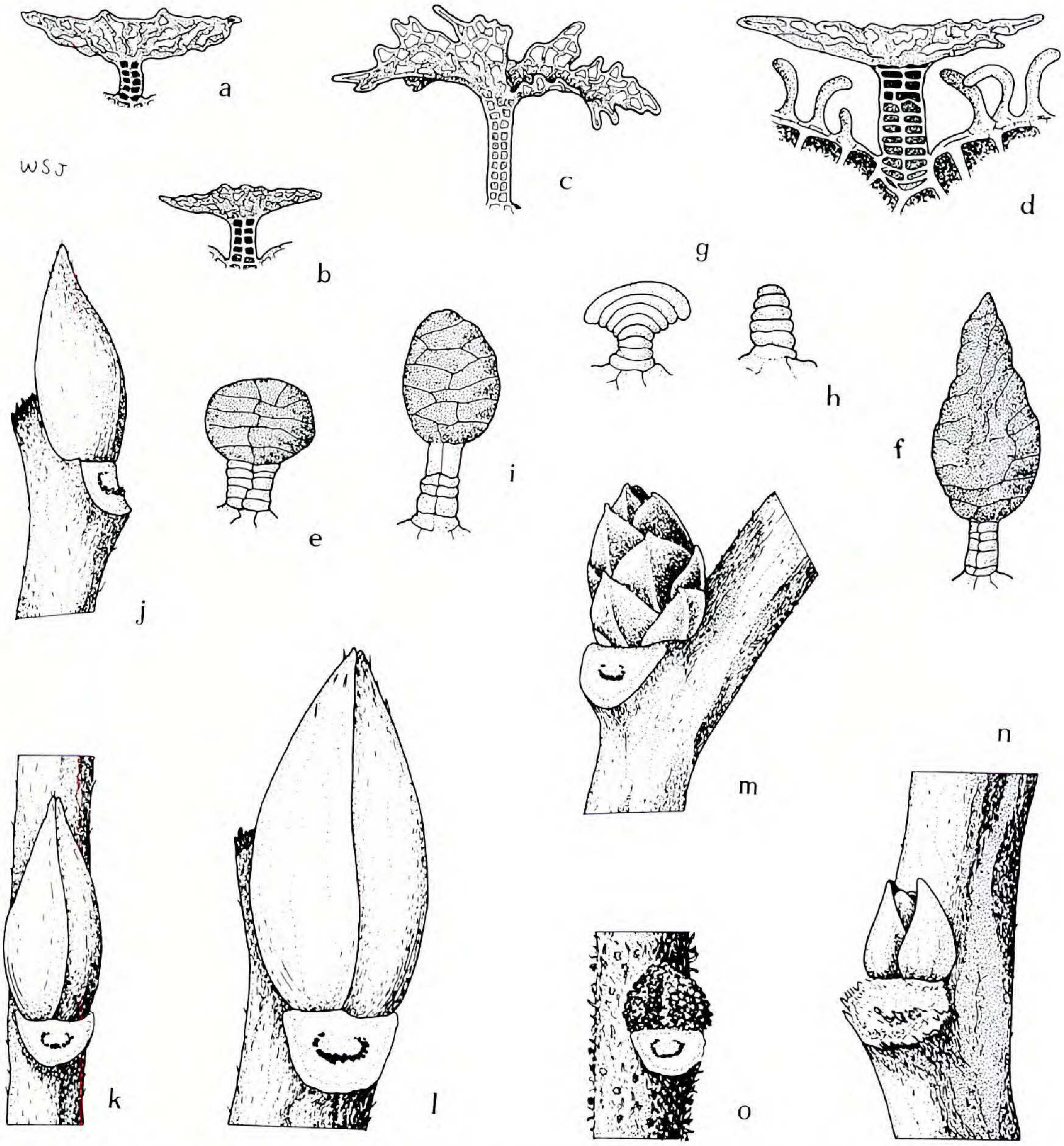

FIGURE 10. Hairs and buds. a–i, hairs, from abaxial leaf surface, × 150: a, *Lyonia truncata,* peltate scale; b, *L. alainii,* peltate scale; c, *L. latifolia,* peltate scale; d, *L. ferruginea,* peltate scale and adjacent unicellular hairs; e, f, *L. lucida,* multicellular hairs; g, h, *L. lucida,* developing multicellular hairs; i, *L. mariana,* multicellular hair. j–o, buds, × 5: j, k, *L. ligustrina* var. *ligustrina;* l, *L. ovalifolia* var. *ovalifolia;* m, *L. mariana;* n, *L. lucida;* o, *L. fruticosa.*

species (e.g., *L. truncata, L. rubiginosa, L. latifolia, L. nipensis*) have leaves that vary from rounded to truncate, obtuse, or acute (and in some, even acuminate) at the apex. In populations of *L. ferruginea* and *L. fruticosa* on the Coastal Plain in Georgia and Florida, plants with rounded leaves and plants with acute leaves have been seen growing side by side (pers. obs.). The variation in leaf apex is slightly less in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS, but even in these groups it is often considerable. *Lyonia ovalifolia, L. villosa,* and *L. ligustrina* are particularly variable (FIGURES 21–28). Narrowly to widely obovate, ovate, or elliptic leaves are commonly found in the same species. However, a few taxa have unusually shaped leaves. The lamina of *L. heptamera* is cordate at the base, while that of *L. buchii* is cuneate—a difference that helps in distinguishing the two species. Similarly, the narrowly elliptic lamina of *L. glandulosa* var. *revolutifolia* can be distinguished from that of var. *glandulosa,* which is narrowly to widely obovate. In spite of the wide range of variation in leaf size and shape or in apex type that is found in many taxa, these characters employed with caution are often useful in differentiating the varieties of several Eastern Asian and West Indian species; they also help to separate some species (e.g., *L. microcarpa* from *L. urbaniana,* and *L. compta* or *L. chapaënsis* from the remaining Asian species). The leaf blade is more or less flat in most species, but it may be strongly recurved as in *L. nipensis* var. *depressinerva, L. glandulosa,* and *L. ferruginea.* The margin is at least occasionally slightly revolute in most species, but in a few it is strongly so. It is entire in all taxa of sects. MARIA and PIERIDOPSIS, although slightly undulate in *L. chapaënsis.* The leaves of *L. ligustrina* are minutely serrulate, and those of species of sect. LYONIA vary from entire, to obscurely toothed, to irregularly and clearly toothed or notched. The teeth are usually more prominent toward the distal end of the blade, and each tooth has a multicellular, swollen-headed hair (or, in sect. LYONIA, a peltate scale) on its distal side. The leaves of Cuban and Jamaican species tend to be entire margined, while those of Hispaniolan and Puerto Rican species are often distinctly toothed. The number of teeth is helpful in differentiating *L. rubiginosa* var. *costata* from var. *stahlii,* and *L. maestrensis* from several other Cuban species.

The veins of the leaves of most species are either only very slightly raised above the surface or slightly depressed. However, in some species (*Lyonia nipensis* var. *depressinerva, L. ferruginea, L. glandulosa, L. rubiginosa* var. *costata, L. latifolia* var. *latifolia, L. buchii,* and *L. heptamera*) the first-, second-, and sometimes even third- or higher-order veins are often prominently impressed into the adaxial leaf surface (see FIGURES 35, 44, and 50). *Lyonia heptamera, L. buchii, L. urbaniana, L. tinensis,* and *L. microcarpa* are unusual in that the veins on the abaxial leaf surface form a raised network, thus forming small pockets in the surface of the leaf. When seen in cross section (see FIGURE 31), the leaves often seem to have lacunae of epidermal cells, hairs, and stomata inside the mesophyll tissue, but actually such chambers are always connected with the outside. The stomata of these species are often limited to the lacunae. *Lyonia latifolia* var. *latifolia* (high-elevation forms) and *L. alpina* also rarely form such pockets.

The leaf venation pattern varies from brochidodromous (FIGURE 21) to eucamptodromous (FIGURE 24) or rarely more or less acrodromous (FIGURE 27, g) (see TABLE 8; Hickey, 1973; Dilcher, 1974; Melville, 1976). This character is often useful in identifying the Asian taxa. All species of sects. LYONIA and ARSENOCOCCUS have leaves with brochidodromous venation. The leaves of *L. lucida* are unique in having an intramarginal vein. Differences in the angle of divergence of the secondary veins and in their prominence and curvature near the margin are helpful in distinguishing taxa, especially in sect. PIERIDOPSIS (FIGURES 21–24, 27).

The third-order veins vary from reticulate to percurrent, with the former being the more common condition (TABLES 7, 8). *Lyonia buchii* and *L. heptamera* are unusual in that they are the only species of sect. LYONIA that often have percurrent tertiary veins. Percurrent veins are more common in *L. mariana, L. ligustrina,* and especially in sect. PIERIDOPSIS. They usually form an oblique angle with the midrib but often vary from parallel to perpendicular with it in different parts of the leaf.

The higher-order veins are reticulate, the areoles are usually isodiametric in shape, and the vein endings simple or forked to dendroid (FIGURES 17, 18). The vein endings are surrounded by a sheath of lignified, isodiametric cells (see Lems, 1964) that stain darkly in sects. ARSENOCOCCUS and PIERIDOPSIS and in *L. mariana,* and that give the end a blunt appearance; they are usually difficult to see in sect. LYONIA (TABLE 8), so the end looks pointed. The ultimate veins of the generalized species of sect. LYONIA are often slender and tend to have blunt endings (FIGURE 17). However, the anatomically specialized *L. buchii* and *L. heptamera* also tend to have blunt vein endings.

The density of the ultimate venation and the size of the areoles is rather variable within the genus, but these characters have not been quantified. The areoles are especially small in *Lyonia macrocalyx* and in some varieties of *L. ovalifolia.* The morphologically specialized species of sect. LYONIA often have strongly thickened high-order veins (FIGURE 18). The areoles of such taxa in this group as *L. tuerckheimii* and *L. alainii* are rounded, while those of others such as *L. nipensis, L. obtusa,* and *L. macrophylla* are angular. It is of interest that the generalized species *L. affinis* has angular areoles, indicating a relationship to more specialized Cuban species (such as *L. obtusa*), while the generalized *L. rubiginosa* has more or less rounded areoles and is thus likely closer to *L. tuerckheimii.* In general, venation characters strongly reinforce the taxonomic groupings derived from a consideration of other criteria.

The adaxial leaf epidermis of some Caribbean species (e.g., *Lyonia glandulosa, L. urbaniana,* and *L. heptamera*) is often rough with the persistent bases of peltate scales, but in most species it is quite smooth, and lustrous or dull. *Lyonia ovalifolia* (sometimes), *L. villosa* (usually), and *L. macrocalyx* (always) have glaucous abaxial leaf surfaces.

INFLORESCENCES

The flowers of *Lyonia* are borne in axillary fascicles, racemes, or panicles on branches of the previous or (less commonly) the present season (see

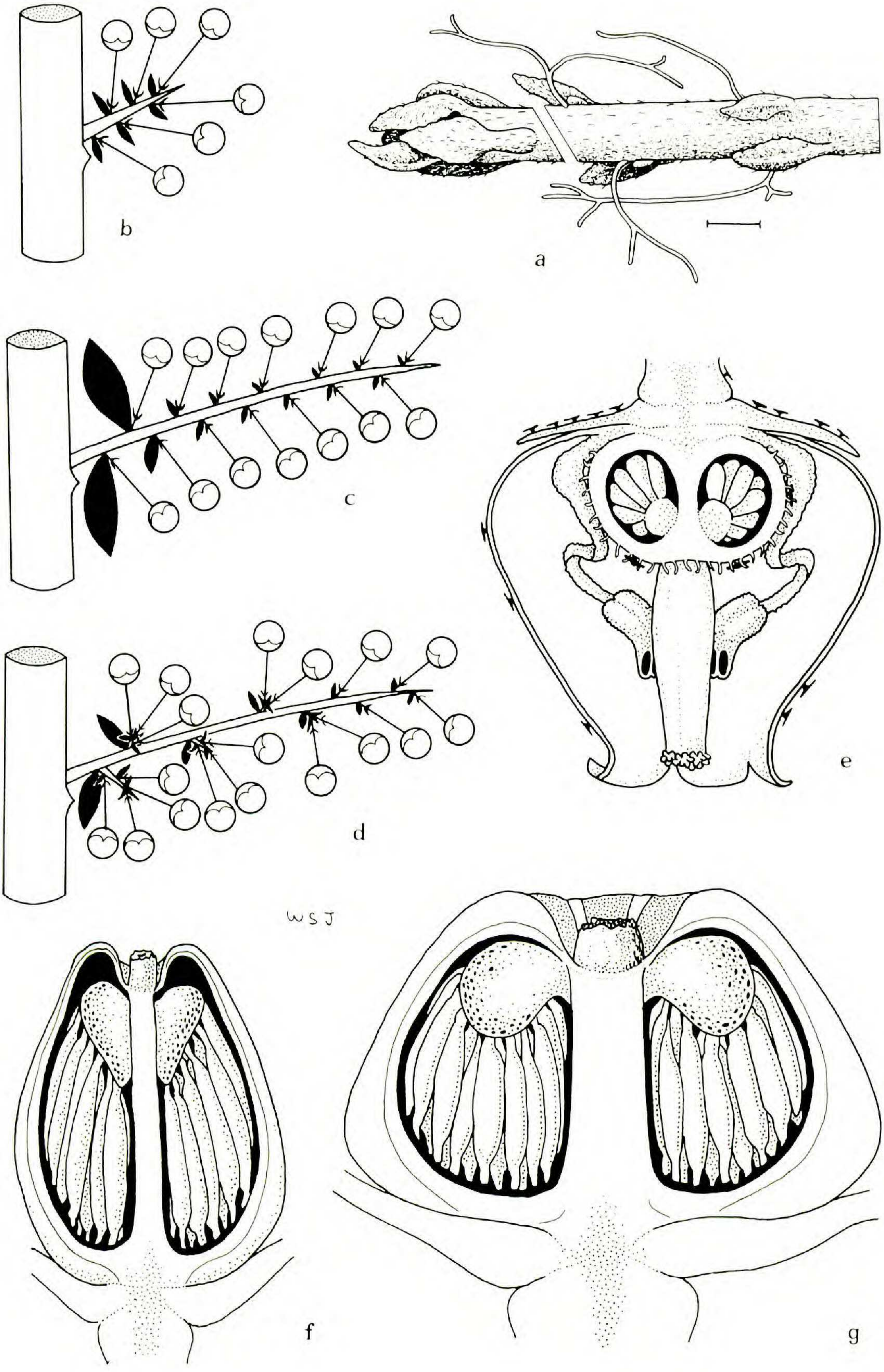
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FIGURE 11, and Lems, 1962). In *Lyonia* there is always one inflorescence per leaf axil. The species of sects. LYONIA and MARIA characteristically bear flowers in fascicles, although *L. heptamera, L. buchii,* and occasionally *L. fruticosa* and *L. tuerckheimii* have short racemes. All the species of sect. PIERIDOPSIS have racemes; in some species these reach 10–20 cm. in length. However, *L. villosa* often tends to have very short racemes, a trend that, if continued, would result in fascicles similar to those of sect. MARIA. The flowers are borne spirally on these horizontal to slightly ascending racemes, but since the flowers are pendulous, they make the racemes appear one sided or secund. In *L. compta,* the racemes are rigidly ascending, and the pendulous flowers are positioned on all sides. The inflorescence of *L. ligustrina* (sect. ARSENOCOCCUS) is the most complex of the genus; it is a raceme of fascicles or of short racemes (subpaniculate). Toward the apex of the inflorescence, the fascicles (or racemes) become progressively reduced, and near the end they are often represented by only solitary flowers (FIGURE 11). There are no terminal flowers in any of these inflorescence types; the apex of the raceme or fascicle simply aborts. They are thus polytelic (see Weberling, 1965). The fascicles occurring in sect. MARIA and in most of the species of sect. LYONIA are probably derived from racemes through a shortening of the inflorescence axis. *Lyonia ligustrina,* with its complex, subpaniculate inflorescence, may also have evolved from ancestors with racemose inflorescences through compression of the morphological structures of two growing seasons into one, or by reduction of a paniculate inflorescence.

The primitive inflorescence type in *Lyonia* is thus possibly a raceme, although it is likely that this is not primitive within the Ericaceae as a whole. According to Weberling (1965), the polytelic inflorescence type is more highly evolved than the monotelic type. Within the Andromedeae, only *Craibiodendron* has inflorescences with terminal flowers; thus, the inflorescence of *Craibiodendron,* a large panicle, is possibly primitive within the tribe.

MORPHOGENETIC CYCLE

As in most other members of the Andromedeae, the shoot meristem in *Lyonia* has a limited life span, and growth in height is achieved by a succession of lateral buds rather than by continuous growth of a terminal meristem (see Lems, 1962). In *Lyonia* a vegetative branch, which has vegetative and floral buds variously arranged, is formed in the spring and early summer. In sects. MARIA and ARSENOCOCCUS the floral buds are usually above the vegetative ones; in species of sect. PIERIDOPSIS except *L. compta,* they are usually below; and in sect. LYONIA the two are often somewhat intermixed, although the floral buds are usually borne toward the apex of the shoot.

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FIGURE 11. a, horizontal underground rhizome of *Lyonia ligustrina* var. *ligustrina* (scale = 1 mm.). b–d, diagrammatic inflorescences: b, *Lyonia* sects. LYONIA and MARIA; c, *Lyonia* sect. PIERIDOPSIS; d, *Lyonia* sect. ARSENOCOCCUS. e, diagrammatic longitudinal section of flower of *L. fruticosa.* f, g, longitudinal sections of capsules, × 7.5: f, *L. ferruginea;* g, *L. heptamera.*

Each floral bud contains an embryonic inflorescence in which the individual flowers are as yet incompletely differentiated. No pollen or ovules can be distinguished before winter. In the spring these buds open, the inflorescence emerges, and the flowers mature; meiosis thus occurs in the spring. At this time, or soon after, the vegetative buds open and new vegetative shoots that continue the cycle begin to grow. Fruit maturation occurs during the summer, and the seeds are mature by fall. The capsules are persistent, and the seeds are dispersed throughout the winter and the following spring and summer. In sect. LYONIA periodicity of growth is less clear, as might be expected in plants from tropical or subtropical climates, and *L. heptamera* and *L. buchii* branch and flower almost continually. *Lyonia fruticosa* is unusual in that its inflorescences and flowers are formed mainly on the shoots of the present season (although some flowers are usually also produced on branches of the previous year). As the shoots grow out in the spring, some of their axillary buds immediately develop inflorescences; thus, flowering occurs soon after the young shoots are produced (from spring to summer). Dormancy of floral buds in some temperate species such as *L. mariana* and *L. ovalifolia* is often prematurely broken, and occasional plants can be found in flower in the autumn.

FLORAL BRACTS AND BRACTEOLES

In all species of *Lyonia,* the pedicel is subtended by a single bract. The size of this bract varies from only 2–3 mm. long to large (ca. 11 cm.) and foliaceous. In sects. LYONIA and MARIA the bracts are usually all very small and caducous or deciduous, but in sects. ARSENOCOCCUS and PIERIDOPSIS they vary from minute and caducous (near the apex of the inflorescence) to foliaceous and persistent (toward the base). The size, number, and position of these foliaceous bracts is helpful in differentiating the varieties of *L. ovalifolia* and *L. ligustrina,* and in separating *L. compta* from the remaining Asian species.

Each pedicel in *Lyonia* has a pair of bracteoles. They are usually located at or near the base of the pedicel and are characteristically minute, linear to triangular (or, less commonly, ovate), and less than 1 to (at most) 6 (e.g., *Lyonia heptamera* and *L. macrocalyx*) mm. long. The bracteoles are opposite and at the base of the pedicel in sects. PIERIDOPSIS, ARSENOCOCCUS, and MARIA, while in sect. LYONIA they vary from opposite and basal to (in a few species) often alternate and on the lower fifth of the pedicel. The bracteoles are often caducous in sects. LYONIA, PIERIDOPSIS, and ARSENOCOCCUS but are usually persistent in sect. MARIA. The size, shape, and position of the bracteoles are, in general, too uniform to be useful at the specific level.

FLOWERS

All species have actinomorphic, perfect, pendulous flowers, although the pedicel curves upward as the fruits begin to develop, ultimately placing the capsules in an erect position. The flowers of most species are five-merous, but in a few (e.g., *L. heptamera* and *L. buchii*) they are consistently six- or seven-merous, and in several others (see keys) they are usually four-merous.

This latter character has evidently evolved several times because species with four-merous flowers are independently related to species with five-merous ones. In some predominantly five-merous species (e.g., *L. rubiginosa, L. latifolia,* and *L. urbaniana*), individuals with a mixture of five- and four-merous, or all four-merous, flowers are found; occasionally the reverse occurs (as in *L. myrtilloides*). *Lyonia fruticosa* usually has five-merous flowers, but individuals with a mixture of five-, six-, and seven-merous ones can often be found. Thus, numerical variation—although a useful taxonomic character—must be used with care.

PEDICEL. The pedicel varies in length from only 1.5–4.5 mm., as in *Lyonia octandra* and *L. trinidadensis,* often up to 20–30 mm., as in *L. obtusa* and *L. nipensis.* Pedicel length is not a very useful taxonomic character, since the pedicel tends to elongate as the flower and fruit develop. Nearly all species have a clearly developed articulation (or at least a slight constriction) between the pedicel and the calyx, but in *L. glandulosa* and *L. toaënsis* the pedicel and calyx join smoothly.

CALYX. The calyx is composed of four to seven (or rarely eight) sepals that are connate only at the very base. The calyx lobes can be glabrous to densely pubescent or lepidote, and they are usually persistent, except in *Lyonia mariana* (and sometimes in *L. macrocalyx*), in which they fall with the leaves. (*Lyonia macrocalyx* is also unusual in that it has expanded and subfoliaceous lobes, which may be variously notched at the apex.) Stomata are usually present only on the abaxial surface. The lobes show a marked interspecific variation in length (for example, 0.5–1.5 mm. in *L. ligustrina* and 4.5–9(–11) mm. in *L. macrocalyx*). They are valvate in the buds of sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS, but are slightly imbricate in sect. LYONIA. In some taxa (e.g., *L. lucida* and *L. mariana*) they are slightly swollen near the base. The apex varies from acuminate to acute, obtuse, or rounded, but is usually acute to acuminate in sect. LYONIA.

COROLLA. The corolla is always sympetalous and deciduous. It is usually thin and delicate, except in *Lyonia heptamera, L. buchii, L. nipensis, L. obtusa,* and *L. latifolia,* where it is rigid and fleshy. Stomata are nearly always present on the outer surface but lacking on the inner. The corolla varies in shape from cylindrical to elongate-urceolate, shortly urceolate, globose, or more or less campanulate, with four to seven (or rarely eight) usually short, imbricate lobes. *Lyonia buchii* is unusual in having well-developed corolla lobes, often 4 mm. long, and *L. lucida* is unique in that its corolla is cylindrical with a swollen base. The corolla is most often white, or white with a pinkish tinge toward the mouth, but occasional pink forms occur. *Lyonia lucida* characteristically has pink (to even reddish) corollas. The size of the corolla varies considerably, from 2–3 mm. long and 1–2.2 mm. wide in *L. glandulosa* to 8–13 mm. long and 8–13 mm. wide in *L. heptamera.* The shape, size, and color of the corolla are all useful taxonomic criteria in *Lyonia* (see keys for examples).

The multicellular hairs that characterize each section also occur on the outside of the corolla, and the density of these hairs is useful in distinguishing a few Cuban species such as *Lyonia latifolia* and *L. nipensis*. Very rarely, there are also a few unicellular hairs on the outside of the corolla; these are most common in the western populations of *L. mariana*. The inner surface is always completely glabrous.

ANDROECIUM. The flowers of all species of *Lyonia* have twice as many stamens as corolla lobes (i.e., 8 to 14, rarely 16). They are arranged in two whorls that occasionally differ slightly in size, and are inserted at the base of the corolla; the outer whorl is opposite the corolla lobes. The stamens are always included and are arranged in a tight ring, with the anther pores facing inward and pressed against the style (FIGURE 11). (In addition, they show the peculiar characters of the ericaceous stamen—see Artopoeus, 1903; Matthews & Knox, 1926). The filaments are slender, flattened, geniculate, and slightly to markedly swollen near the base. They are roughened in all species of sect. LYONIA and in *L. lucida*, but in *L. ligustrina*, *L. mariana*, and most species of sect. PIERIDOPSIS, they have long, unicellular hairs, at least near the base. *Lyonia chapaënsis* is unusual in that its filaments sometimes lack unicellular hairs and are papillose. *Lyonia villosa* very rarely has a few large, multicellular hairs on the filaments (FIGURE 9). Filament length varies from only 1–1.5 mm. in *L. glandulosa* to as long as 9 mm. in *L. ovalifolia;* it is strongly correlated with flower size.

A pair of spurs is present near the apex of the filament in many species of all four sections of the genus, although those of species such as *Lyonia ligustrina* are minute and often overlooked. The presence of filament spurs is a character that is taxonomically useful in distinguishing a few Asian species, although it must be used with caution since some species vary infraspecifically in this character. The position at which the spurs are borne is also quite variable: they can occur on the upper portion of the filament to just below the anther-filament junction, but they are never on the back of the anther itself (FIGURES 20, 22, 24, 25, 29, 30, 34, 49). All species have disintegration tissue that breaks down as the stamen matures to produce a white, powdery substance (Palser, 1951) on the back of each anther lobe, extending at least along the apex of the filament and along the upper edge of the spurs (when these are present). The anthers are papillose (especially toward the base), have four microsporangia, and open by two introrse-terminal (but morphologically basal) elliptic pores. The anthers lack apical awns but are slightly apiculate. These apiculae seem to be formed during the dehiscence of the anther and are not present as identifiable structures before this process.

GYNOECIUM. The stigma is truncate to capitate, obscurely four- to seven- (or eight-)lobed, and minutely papillose. The lobes are alternate with the loculi of the ovary. The style is columnar, glabrous, straight, and with a four- to seven- (or eight-)fluted central canal; it is impressed into the apex of the ovary. The length of the style is strongly correlated with the size of the corolla and has thus not been used taxonomically. A swelling near the base of the style may be developed in many taxa; it may be of taxonomic importance, but further investigations are needed since it is difficult to observe

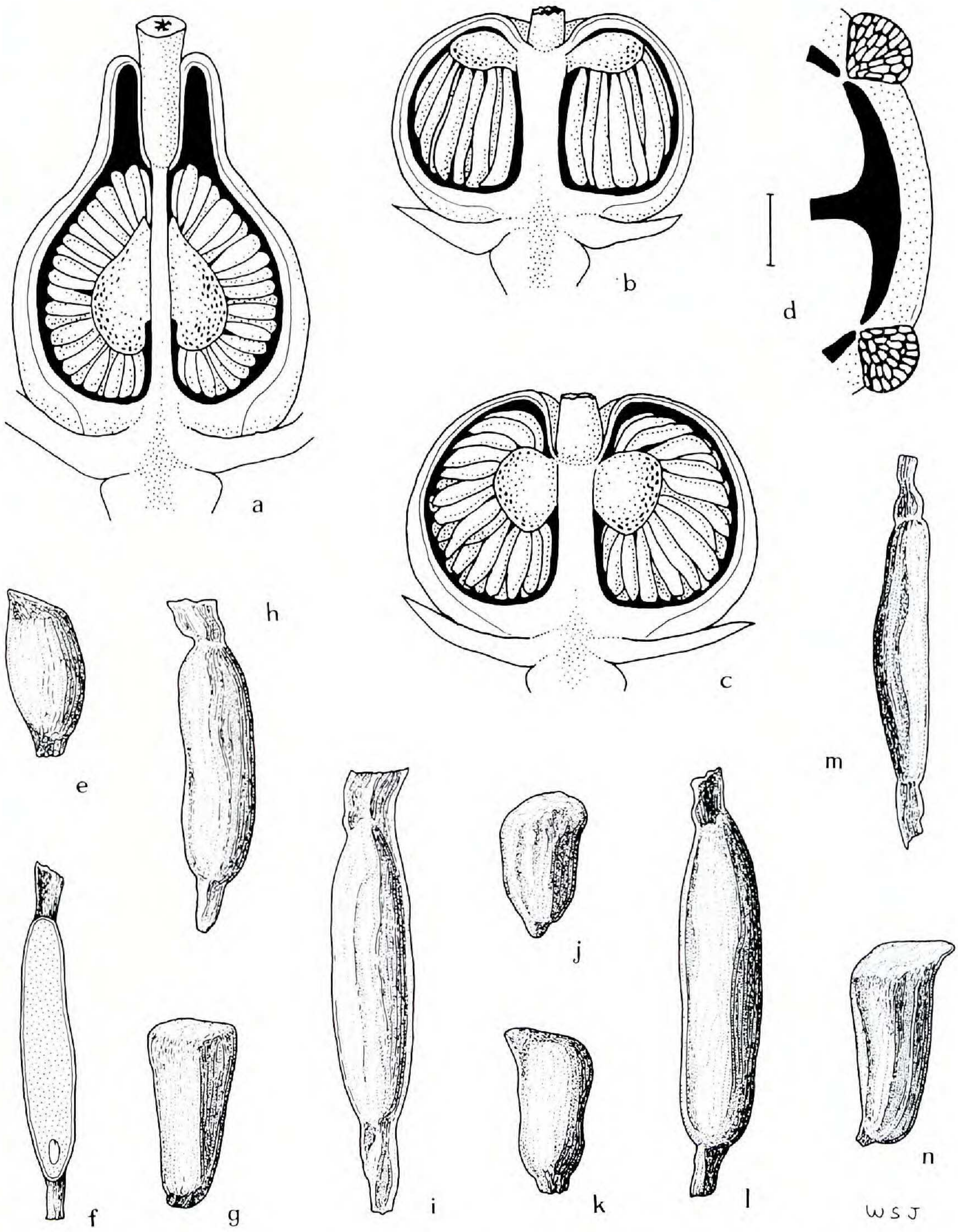

FIGURE 12. Fruits and seeds of *Lyonia.* a–d, capsules. a–c, longitudinal sections, × 7.5: a, *L. mariana;* b, *L. ligustrina;* c, *L. ovalifolia* var. *ovalifolia.* d, *L. mariana,* cross section of single valve and two adjacent sutures (scale = 0.5 mm.). e–n, seeds, × 20: e, *L. ovalifolia* var. *ovalifolia;* f, *L. fruticosa,* longitudinal section showing embryo and endosperm; g, *L. mariana;* h, *L. tuerckheimii;* i, *L. heptamera;* j, *L. lucida;* k, *L. villosa* var. *sphaerantha;* l, *L. nipensis* var. *nipensis;* m, *L. fruticosa;* n, *L. ligustrina* var. *ligustrina.*

TABLE 6. **Chromosome numbers of Lyonia.**

SPECIES	*n*	COLLECTION	LOCALITY
L. truncata var. *montecristina*	12	*Judd 1341* (A)	Dominican Republic, Cordillera Central, S. of El Rubio, ca. 640 m.
L. truncata var. *truncata*	12	*Judd 1478* (A)	Dominican Republic, Sierra de Baoruco, S. of Aceitillar, ca. 1000 m.
L. heptamera	12	*Judd 1214* (A)	Dominican Republic, Cordillera Central, near Valle Nuevo, ca. 2150 m.
L. octandra	12	*Judd 658* (A)	Jamaica, near Blue Mountain Peak, ca. 2130 m.
L. fruticosa	12	*Judd 1963* (A)	Greenhouse plant, originally collected in Long Co., Georgia (*Judd 325*)
L. ligustrina var. *ligustrina*	12	*Judd 1663* (A)	Massachusetts, Ponkapoag Bog, Canton, Middlesex Co.

in dried material. The ovary is superior, four- to seven- (or eight-)locular, and glabrous to densely covered with unicellular hairs, peltate scales, or glandular hairs. The placentae are axile and are borne subapically to nearly "basally" on a central columella. Species with nearly basal placentae have very deeply impressed styles; the placentae are thus still apical with regard to the position of the junction between the style and ovary (FIGURES 11, 12). The placentae are very slightly bilobed and bear numerous anatropous ovules. The ovules have a single integument and a single-layered, evanescent nucellus; the gametophyte development is of the Polygonum type (see Palser, 1952). The species of sect. LYONIA have fewer ovules (and seeds) per locule than do those of the remaining sections. The shape of the ovary varies from

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FIGURE 13. Petioles and pith cells of *Lyonia*. a–e, cross sections of petioles, × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, parenchyma cells with stipples). a, *L. mariana*, upper petiole. b, c, *L. lucida:* b, near base of petiole; c, upper petiole. d, *L. ferruginea*, mid-petiole. e, *L. macrophylla*, upper petiole. f, g, diagrammatic representations of pith cells from branches (greatly enlarged): f, homogeneous (*L. truncata*); g, heterogeneous (*L. ligustrina*).

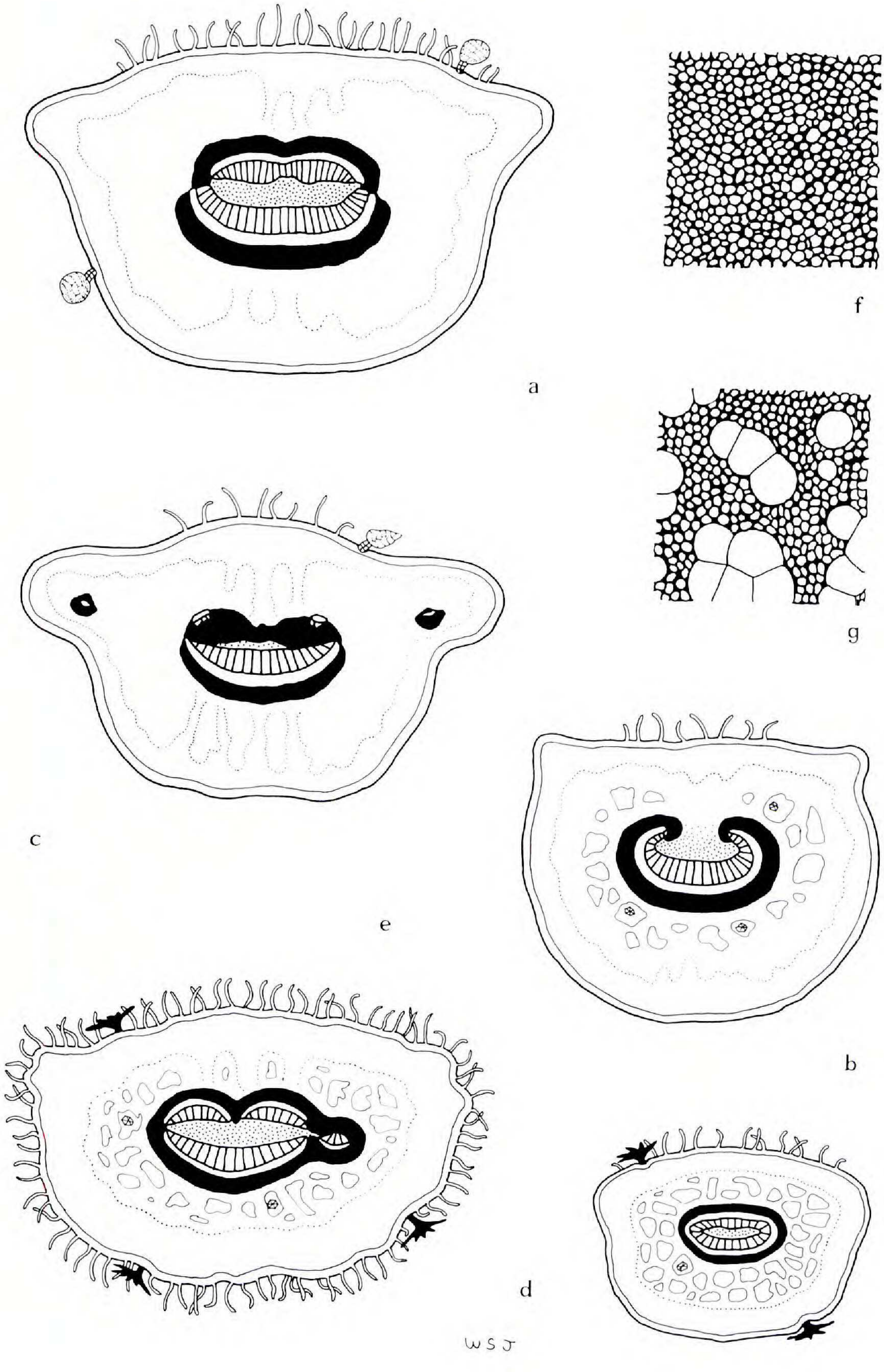
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TABLE 7. **Key to symbols and character abbreviations used in Table 8.**

SYMBOL	CHARACTER	ABBREVIATION	MEANING
A	Pith type (stem)	+	Heterogeneous
		–	Homogeneous
B	Lignification of leaf epidermis	I	Inner periclinal walls lignified but not strongly thickened
		II	Inner periclinal walls lignified and strongly thickened
		–	Not lignified, or only slightly lignified over major veins
C	Height : breadth ratio of adaxial leaf epidermal cells	Ratio	
D	Leaves with adaxial hypodermis of at least 1 cell layer	+	Yes
		(+)	Sometimes (or partial hypodermis)
		–	No
E	Adaxial hypodermis of 2 cell layers	+	Yes
		(+)	Partial
		–	No
F	Vascular bundle of petiole	I	Bifacial, usually forming cylinder
		II	Bifacial, forming cylinder including medullary bundles
		III	Bifacial, usually not joining to form cylinder
		IV	Unifacial
G	Veins of abaxial leaf surface forming raised-reticulate pattern	+	Yes
		–	No
H	Leaves usually with dense layer of unicellular hairs on abaxial surface	+	Yes
		–	No
I	Leaves papillose on abaxial surface	+	Yes
		–	No
J	Type of multicellular hairs	I	Peltate scales
		II	Short-headed hairs
		III	Long-headed hairs

TABLE 7 (*continued*).

SYMBOL	CHARACTER	ABBREVIATION	MEANING
K	Peltate scales sunken into abaxial leaf epidermis	+	Yes
		–	No
L	Pattern of lignified cells surrounding major leaf veins	I	Transcurrent veins
		II	Semitranscurrent veins
		III	Embedded veins
M	Pattern of major secondary leaf veins	+	Brochidodromous
		–	Eucamptodromous
		*	Extending to intramarginal vein
N	Pattern of 3° veins	+	Reticulate
		–	Percurrent
O	Vein endings	I	Surrounded by prominently staining cluster of lignified cells (thus appearing blunt)
		II	Not surrounded by prominently staining cells (thus appearing pointed)
P	Mesophyll tissue of leaves	+	1 or 2 layers of spongy cells lignified near abaxial epidermis
		–	Cells not lignified

ovoid to globose or subglobose, but this variation is better expressed in the mature fruit. A nectariferous disc is variously developed around the base of the ovary. A few stomata are often present.

FRUITS AND SEEDS

The fruit of *Lyonia* is a four- to seven- (or eight-)angled, subglobose, globose, narrowly to widely ovoid, ellipsoid, or urn-shaped, loculicidal capsule, with prominent, pale, thickened sutures that often separate from the adjacent valves in dehiscence (FIGURES 29, 34, 46, 48, 49). These thickened sutures are formed from a band of lignified cells running down the middle of the outside carpel wall (FIGURE 12) and are best developed in sect. LYONIA. The capsules of *Lyonia,* with their prominent sutures, are unique within the Ericaceae. *Lyonia compta* and *L. chapaënsis* are unusual in that they lack (or very nearly lack) these peculiar structures.

The size and shape of the capsules tend to be rather constant within a

TABLE 8. **Variation of selected anatomical and indumentum characters in Lyonia.***

TAXON (SPECIES NUMBER)	CHARACTER CODE															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1	-	-	±1	+	-	III	-	-	-	III	NA	III	+	+,-	I	-
2	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+,-	+,-	I	-
3A	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+	-	I	-
3B	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+	-	I	-
3C	-	-	.5-1	-	-	I, III	-	-	+	III	NA	III	+	-	I	-
3D	-	-	.5-1	-	-	I, III	-	-	+,-	III	NA	III	- (+)	-	I	-
3E	-	-	.3-.5	-	-	III	-	-	-	III	NA	III	-	+,-	I	+
3F	-	-	.5-1	-	-	III	-	-	-	III	NA	III	-	-	I	+
3G	-	-	1-2	-	-	I, III	-	-	-	III	NA	III	-	+,-	I	+
4A	-	-	.5-1	-	-	III	-	-	+	III	NA	III	+	-	I	-
4B	-	-	±1	-	-	III	-	-	+	III	NA	III	+	-	I	-
4C	-	-	.5-1	-	-	III	-	-	- (+)	III	NA	III	+	-	I	-
5	-	-	.5-1	-	-	III	-	-	+	III	NA	III	+,-	+,-	I	-
6A	+	-	.3-1	-	-	III	-	-	-	III	NA	III	+	+,-	I	-
6B	+	-	.3-1	-	-	I, III	-	-	-	III	NA	III	+	+,-	I	-
7	-	-	.5-1	-	-	I, III	-	-	-	II	NA	III	+,-	+,-	I	-
8	-	II	.5-1	-	-	III, IV	-	-	-	II	NA	III	*	+ (-)	II	-
9	-	I	±1	+	(+)	II	+	+	-	I	-	II	+	+,-	II	-
10	-	I	1-1.5	+	-	II	+	+	-	I	-	II	+	+,-	II	-
11	-	I	1-2	+	-	I	+	+	-	I	-	I	+	+	II	-
12	-	I	1-3	+	-	I	+	+	-	I	-	I	+	+	II	-
13	-	I	.5-2	+	-	1	+	+	-	I	-	I	+	+	II	-
14	-	I	1-2	+	+ (-)	I	- (+)	+	-	I	+,-	I	+	+	II	-
15A	-	I	1-1.5	+	-	I	-	+	-	I	+	I	+	+	II	-
15B	-	I	.5-2	+	-	I	-	+	-	I	+	I	+	+	II	-
16	-	II	.5-3	(+)	-	I	-	-	-	I	+	I	+	+	II	-
17	-	I	1-1.5	+	+	I	-	-	-	I	+	I	+	+	II	-
18A	-	I	.5-1	+	-	I	-	-	-	I	+	I	+	+	II	-
18B	-	I	.5-1	+	-	I	-	-	-	I	+	I	+	+	II	-
18C	-	I	.5-1.5	(+)	-	I	-	-,+	-	I	+	I	+	+	II	-
19	-	II?	.5-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-

TABLE 8 (*continued*).

TAXON (SPECIES NUMBER)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
20	-	II?	5-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-
21	-	I	.5-1	(+)	-	I	-	-	-	I	+	I	+	+	II	-
22	-	II	.5-1	+	-	I	-	+	-	I	+	I	+	+	II	-
23	-	II	.5-1	(+)	-	I	-	+	-	I	+	I	+	+	II	-
24A	-	II	2-4	(+)	-	I	-	+	-	I	-	I	+	+	II	-
24B	-	II	1-1.5	-	-	I	-	+	-	I	-	III	+	+	II	-
25A	-	II	1-2.5	-	-	I	-	-	-	I	+	III	+	+	II	-
25B	-	II	1-2	-	-	I	-	-	-	I	+	III	+	+	II	-
26	-	II	1-3	-	-	I	-	-	-	I	+	I	+	+	II	-
27	-	II	1-2	+	-	I	-	-	-	I	+	I	+	+	II	-
28	-	II	1-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-
29	-	I	.3-1	-	-	I	-	-	-	I	+	I	+	+	II	-
30A	-	I	±1	+	(+)	I	- (+)	+	-	I	+	I	+	+	II	-
30B	-	I	±1	+	-	I	-	+	-	I	+	I	+	+	II	-
32A	-	II	±1	+	-	I	-	+	-	I	+	I	+	+	II	-
32B	-	II	±1	(+)	-	I	-	+	-	I	+	III, I	+	+	II	-
33	-	I	±1	-	-	I	-	- (+)	-	I	+	III, I	+	+	II	-
34	-	I	±1	-	-	I	-	+	-	I	+	III	+	+	II	-
35	-	I	.5-1	(+)	-	I	-	+	-	I	+	III	+	+	II	-

*For explanation of symbols and character abbreviations, see TABLE 7.

species but often differ greatly between species (FIGURES 28, 29, 34, 38, 41, 52, 56); these differences are very useful in identification. The shape of the capsule is useful in distinguishing among the varieties of *Lyonia ovalifolia* and of *L. villosa*. Other interesting variations in the shape and size of the capsules are evident in the keys.

The seeds are minute, brown, oblong-ovoid to linear or spindle shaped, with the ends drawn into short, sterile extensions or "tails" (in sect. LYONIA; FIGURE 12) or with one end more or less truncated (in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS; FIGURE 12). They are never winged and have a loose, thin testa composed of a single layer of very much elongated cells. The seed morphology is too uniform to be very useful in identifying species in *Lyonia*.


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CYTOLOGY

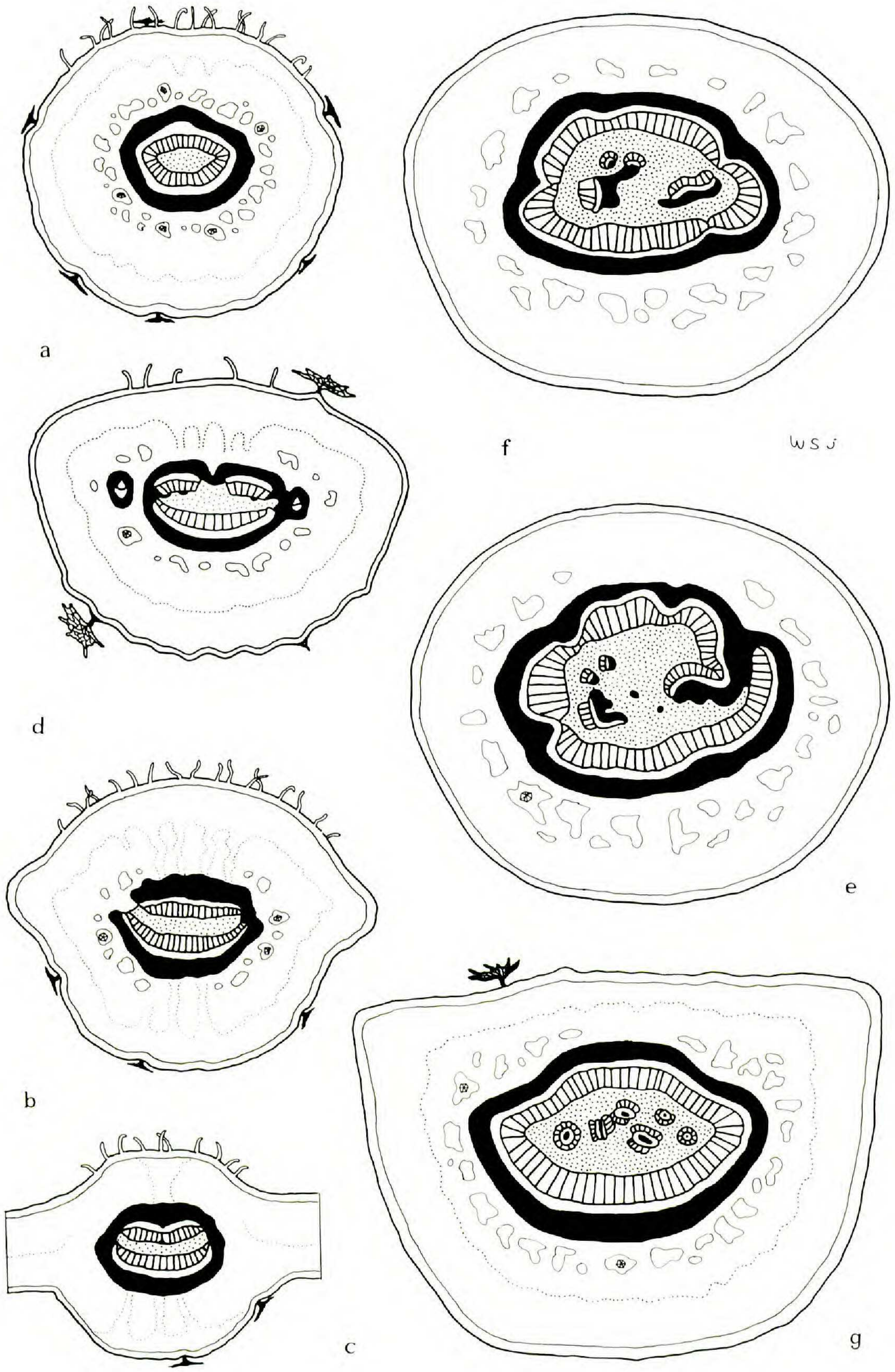
The chromosome numbers of five taxa have been previously recorded. These are *Lyonia mariana*, $2n = 24$ (Callan, 1941); *L. lucida*, $2n = 24$ (Callan, 1941); *L. ovalifolia* var. *foliosa* (reported as *L. foliosa*), $n = 12$ (Larsen, 1966); *L. ovalifolia* (var. *hebecarpa*, since the count was based on Formosan material), $n = 12$ (Chuang *et al.*, 1962); *L. ovalifolia* (var. *ovalifolia*, since the count was based on material from the western Himalayas, India), $n = 12$ (Mehra & Gill, 1968); and *L. ovalifolia* (var. *ovalifolia*, because the count was based on material from Darjeeling, India), $n = 12$ (Mehra & Bawa, 1969).

Meiotic counts have been made of six additional taxa (TABLE 6). Since all species studied have a diploid number of 24, it is likely that there is little variation in chromosome number; this is especially probable since all four sections are represented in these counts, and since only this number has been reported for the related genera *Pieris* and *Agarista* (see Stevens, 1971). All species investigated have very small chromosomes and show normal meiosis. Raven (1975) suggests that 12, which is widespread within the Ericaceae, may be the family's basic chromosome number, with 13 and 11 being frequent aneuploid derivatives.

VEGETATIVE ANATOMY

Selected features of stem, petiole, and lamina anatomy and leaf venation were studied in all species of *Lyonia* in an effort to discover characters that would be useful in delimiting species and/or higher taxonomic groups. Many of these characters had previously been shown to be quite variable, either within the Ericaceae or within other large angiosperm families (see Gris, 1870; Niedenzu, 1890; Metcalfe & Chalk, 1950; Wood, 1961; Lems, 1964; Watson, 1964, 1965; Stace, 1965; Stevens, 1970, 1971; Howard, 1974). The techniques used were extremely simple. Sections were taken through both nodal and internodal regions of young and older stems, and the leaves were sectioned at intervals up the petiole and into the lamina until the apex was reached. Epidermal peels were prepared for some taxa, and all were studied by the acetone-cellulose acetate method described by Payne (1968). Both dried herbarium specimens and material preserved in FAA were used. The herbarium material was softened by boiling and/or soaking in water, and the sections were cut by hand using a razor blade, and stained using phloroglucinol and hydrochloric acid. The leaves of a few species were embedded in paraffin, sectioned on a microtome, dehydrated, stained with

FIGURE 14. Cross sections of petioles and leaf midveins of *Lyonia*, × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, and parenchyma cells with stipples). a–c, *L. ovalifolia* var. *lanceolata:* a, extreme base of petiole; b, lower petiole; c, upper petiole. d, *L. ovalifolia* var. *elliptica,* midvein, ca. lower 1/4 of blade. e, *L. ovalifolia* var. *ovalifolia,* upper petiole. f, g, *L. villosa* var. *pubescens:* f, upper petiole; g, midvein, ca. lower 1/4 of blade. h, *L. ligustrina* var. *ligustrina,* upper petiole.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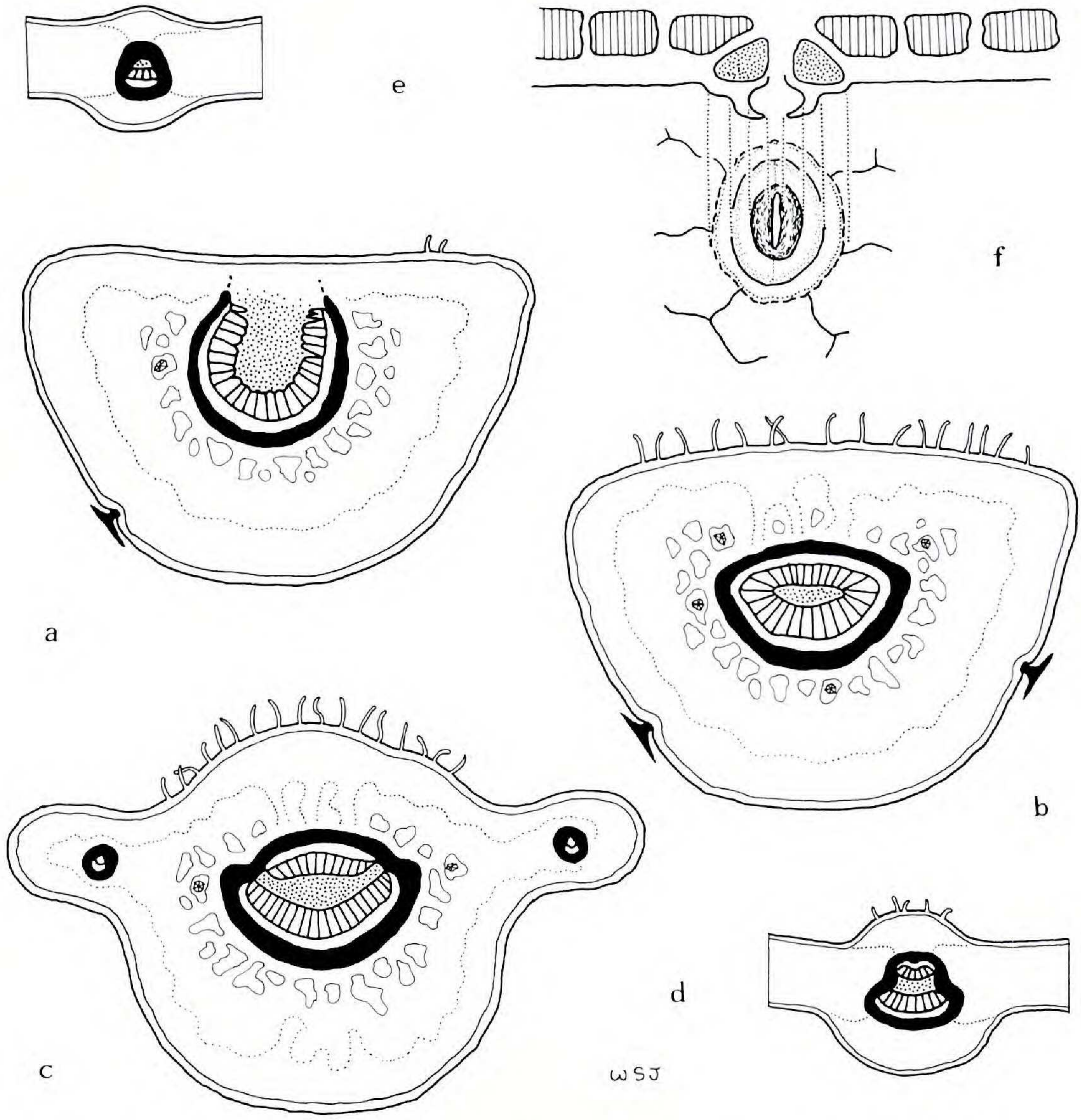

FIGURE 16. a–e, cross sections of petiole and leaf midvein of *Lyonia rubiginosa* var. *costata,* × 25: a, extreme base of petiole; b, lower petiole; c, base of blade; d, midvein, upper 1/4 of blade; e, midvein, near apex. f, diagram illustrating relationship between cross section and surface view of stoma of *L. lucida.*

safranin and fast green, and mounted on slides. Leaves of nearly all taxa were cleared and stained with safranin following the technique of Dilcher (1974). From one to ten leaves (from different specimens) of each species were studied, so in some cases the full range of infraspecific variability

FIGURE 15. Cross sections of petioles of *Lyonia,* × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, parenchyma cells with stipples). a–c, *L. octandra:* a, lower petiole; b, upper petiole; c, midvein, ca. middle of blade. d, *L. urbaniana,* upper petiole. e–g, *L. buchii:* e, near extreme base of petiole; f, slightly distal to e; g, middle petiole.

may not have been determined. In spite of this possible source of error, several very interesting variations in anatomical characters were discovered within the genus.

STEM ANATOMY AND NODAL TYPE

Cox (1948) studied the xylem anatomy of several species of *Lyonia;* wood anatomy was not investigated in the present study. Two major types of pith are present in the stems of *Lyonia* (see L. Watson, 1965; FIGURE 13 and TABLES 7 and 8): heterogeneous (i.e., cells of two distinct sizes intermingled), with the smaller cells having thickened and lignified walls, in *L. ligustrina;* and homogeneous (i.e., all cells more or less the same size, and lignified) in all other species. All species have characteristic fiber bands in the phloem, the lignified bands developing with increasing age of the twig. There is a sheath of fibers in the pericyclic position in all species, and the phellogen is initiated immediately inside this sheath. Clusters of crystals are frequent in the cortex. All species studied have unilacunar nodes.

LEAF ANATOMY

PETIOLE AND MIDRIB. The single vascular bundle of the petiole is arcuate in shape at the base of the petiole but rapidly becomes deeply arcuate and eventually bifacial (see FIGURES 13, 14, 16) toward the apex. In sect. LYONIA (see TABLE 8 and FIGURES 13, 15, 16) the arms of the arcuate bundle fuse to form a complete cylinder of xylem and phloem within the petiole. In the remaining sections the secondary veins usually begin to depart from the sides of the bundle before this fusion has occurred, and this divides the bundle into an adaxial and an abaxial portion (i.e., it is bifacial). The bundle is always bifacial in all species except *Lyonia lucida,* where it is often unifacial although at least sometimes bifacial near the apex of the petiole (FIGURE 13). In sects. ARSENOCOCCUS and PIERIDOPSIS, and in *L. mariana,* there are often two separate strands of xylem and phloem in the adaxial bundle, but this condition is much less common in sect. LYONIA. In all species the bundle eventually becomes unifacial toward the apex of the leaf. *Lyonia heptamera* and *L. buchii* are unique in that they have medullary bundles within the cylinder of xylem (FIGURE 15). These medullary bundles are derived from the inspiraling and fragmentation of a portion of the adaxial side of the xylem cylinder, which then fuses again into a ring, leaving isolated strands composed of xylem, phloem, and fibers inside the re-formed cylinder. The vascular bundle of all species is surrounded by a ring of fibers. The cortex always contains clusters of crystals, which are usually concentrated in the portion next to the vascular bundle. The petiole is generally more or less round in cross section, with the adaxial surface often slightly flattened and sometimes grooved.

LAMINA. Stomata occur only on the abaxial leaf surface and, in general, are not found on the epidermis over the major (i.e., first-, second-, and third-order) veins. They are anomocytic but appear to be surrounded by one or two rings due to the presence of a cuticular ridge or flange surrounding and forming a chamber over the stomatal opening (FIGURE 16). This chamber may function in reducing water loss in the xeric environments in which many

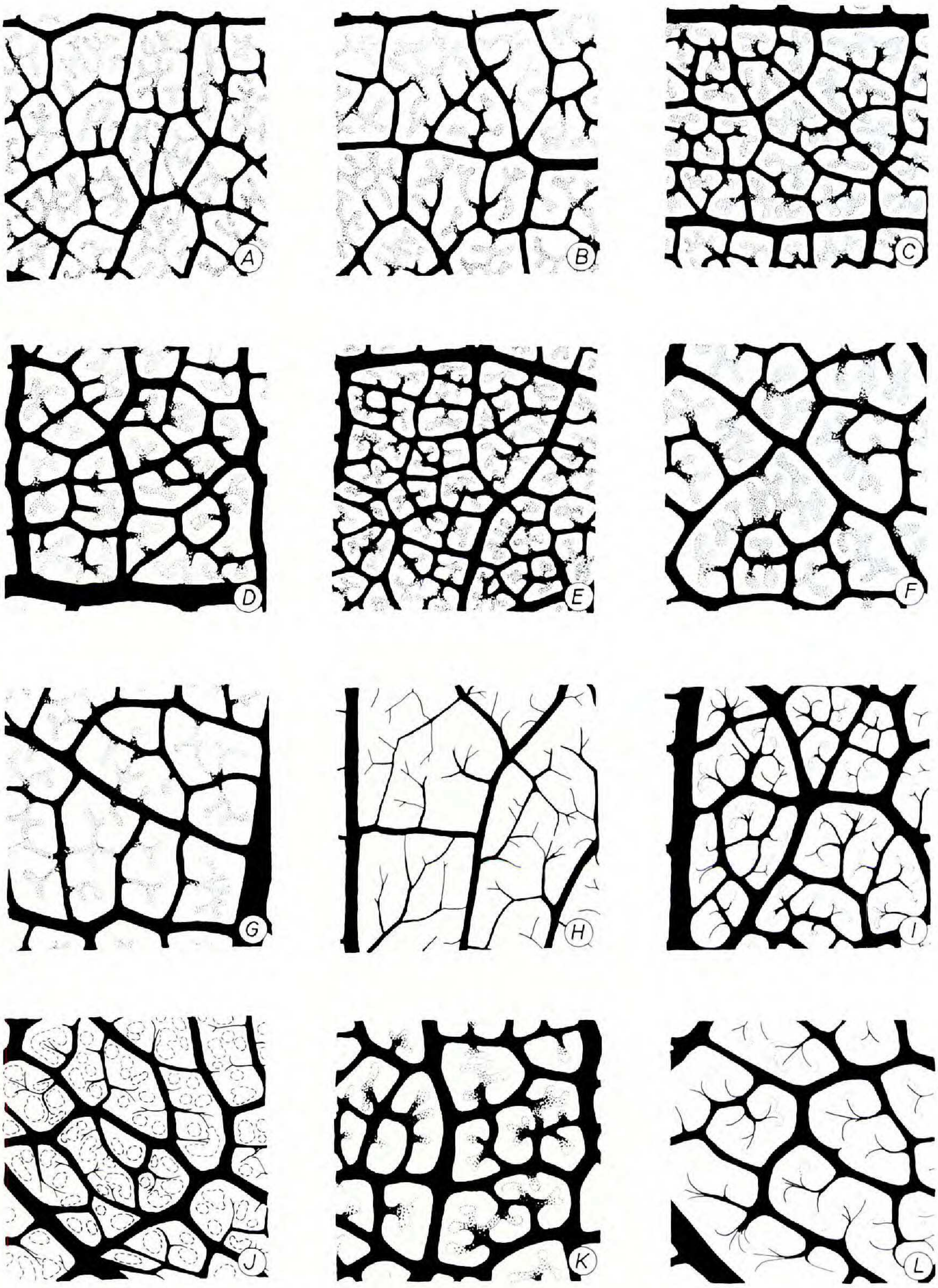

FIGURE 17. Areoles and vein endings of selected species of *Lyonia* (each square = 2.75 sq. mm.): A, *Lyonia ligustrina* var. *foliosiflora;* B, *L. ovalifolia* var. *elliptica;* C, *L. ovalifolia* var. *doyonensis;* D, *L. ovalifolia* var. *lanceolata;* E, *L. macrocalyx;* F, *L. compta;* G, *L. mariana;* H, *L. lucida;* I, *L. truncata* var. *truncata;* J, *L. urbaniana;* K, *L. heptamera;* L, *L. rubiginosa* var. *costata.*

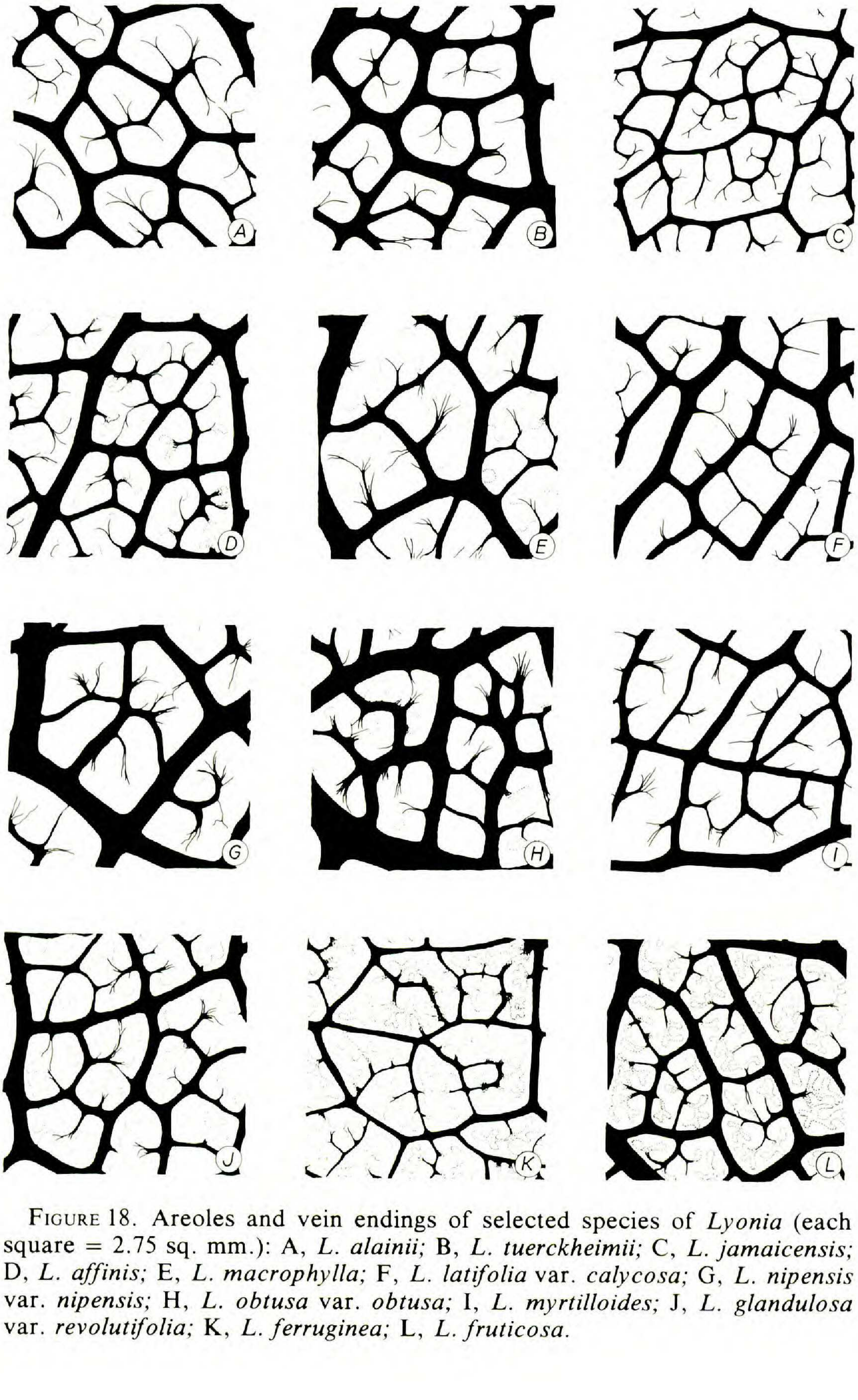

FIGURE 18. Areoles and vein endings of selected species of *Lyonia* (each square = 2.75 sq. mm.): A, *L. alainii;* B, *L. tuerckheimii;* C, *L. jamaicensis;* D, *L. affinis;* E, *L. macrophylla;* F, *L. latifolia* var. *calycosa;* G, *L. nipensis* var. *nipensis;* H, *L. obtusa* var. *obtusa;* I, *L. myrtilloides;* J, *L. glandulosa* var. *revolutifolia;* K, *L. ferruginea;* L, *L. fruticosa.*

species grow. The stomata sometimes show a slight tendency to be oriented with the stomatal aperture parallel to the secondary leaf veins; they also tend to be radially oriented around the bases of the multicellular trichomes, although they are absent immediately adjacent to the bases. Otherwise, orientation is random. The stomata are of several size classes, and small ones, when in the vicinity of a large one, are often arranged with the axes of their apertures pointing toward the larger stoma.

The cuticle is often extremely thick, especially in *Lyonia lucida* and in many species of sect. Lyonia, sometimes reaching slightly over 0.5 mm. In many West Indian taxa it is also often striate, with the striae radially oriented around the peltate scales. The abaxial epidermal cells are usually more or less straight-sided, although they are often somewhat wavy in *L. ligustrina, L. lucida,* some varieties of *L. ovalifolia,* and sometimes *L.*

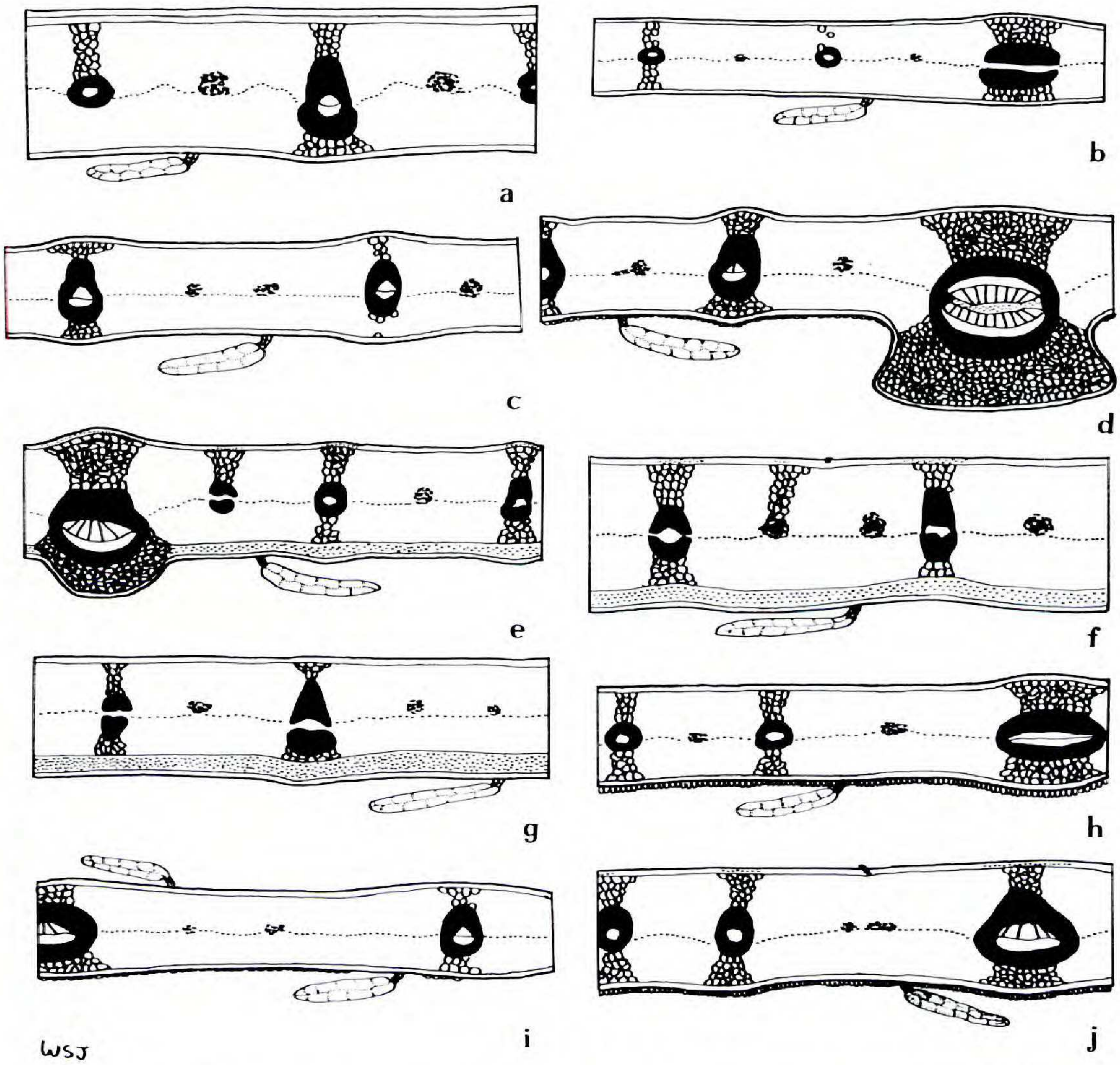

Figure 19. Tranverse sections of leaf blades of various species of *Lyonia* sect. Pieridopsis, × 50 (shaded areas represent lignified cells): a, *Lyonia compta;* b, *L. chapaënsis;* c, *L. ovalifolia* var. *hebecarpa;* d, *L. ovalifolia* var. *doyonensis;* e, *L. ovalifolia* var. *lanceolata;* f, *L. ovalifolia* var. *foliosa;* g, *L. ovalifolia* var. *rubrovenia;* h, *L. macrocalyx;* i, *L. villosa* var. *villosa;* j, *L. villosa* var. *sphaerantha.*

rubiginosa. The adaxial epidermal cells are almost always more or less straight walled. Epidermal cells are usually elongated both over the major veins and in a radial pattern around large, multicellular hairs. When viewed in cross section, they show a wide range of height : breadth ratios (TABLES 7, 8). The epidermal cells are thin walled and unlignified (or are only slightly lignified over the major veins) in the species of sects. PIERIDOPSIS and ARSENOCOCCUS, and in *L. mariana*. The epidermal cells of *L. lucida* are only slightly lignified, but those of the species of sect. LYONIA are usually strongly so. In a related group of Cuban species (TABLE 8), the inner periclinal wall is very prominently thickened and lignified.

Lyonia compta is unusual in that it is the only species among those of sects. PIERIDOPSIS, MARIA, and ARSENOCOCCUS to have a hypodermis (unlignified; see FIGURE 19). Many species of sect. LYONIA (TABLE 8) have a prominent and lignified hypodermis of one or two cell layers (FIGURES 31–33). This character is occasionally of taxonomic importance at the specific level (for example, in distinguishing *L. macrophylla* from *L. ekmanii*, or *L. tuerckheimii* from *L. rubiginosa*). The hypodermis of many species is more strongly developed near the major veins.

Mesophyll tissue is difficult to study from herbarium material, but all species have a well-developed palisade tissue. The number of tiers of cells varies from only one or two (in *Lyonia ligustrina*) to as many as four or five (in *L. lucida*). The walls of the spongy mesophyll cells are usually thin and nonlignified, but in *L. ovalifolia* vars. *lanceolata, foliosa*, and *rubrovenia* one or two layers of spongy tissue next to the abaxial epidermis have thick, lignified walls (FIGURE 19).

The secondary and tertiary veins of many species of sect. LYONIA have no mesophyll tissue either above or below the vascular bundle. In these species the vascular bundle is part of a girder of tissue formed by a group of lignified, thick-walled cells above and below the veins (FIGURES 31–33). This type of "transcurrent" bundle (see Stevens, 1969) contrasts with the vascular bundles of other species (mostly of sects. ARSENOCOCCUS, PIERIDOPSIS, and MARIA; see TABLES 7, 8, and FIGURES 19, 28–30), which are surrounded by chlorophyll-containing mesophyll cells. The bundles of these species are referred to as "embedded." Some species with embedded vascular bundles (e.g., *Lyonia villosa, L. compta, L. macrocalyx*, and some varieties of *L. ovalifolia*) have slightly lignified cells with thin walls and large lumina both above and below the vein, but this condition is quite different from the dense column of lignified, thick-walled, small-lumened cells that occurs in the transcurrent-veined species of sect. LYONIA. *Lyonia buchii* and *L. heptamera* are unusual in that their veins are only semitranscurrent (i.e., the lignified cells surrounding the vascular bundle reach only the adaxial leaf epidermis; FIGURE 31). The pattern of lignified cells surrounding the secondary and tertiary veins is also occasionally useful at the specific or varietal levels; it can be used in distinguishing *L. macrophylla* from *L. obtusa*, or the varieties of *L. nipensis* from each other.

POLLINATION BIOLOGY

From a study of fresh and preserved flowers, it appears that the pollen is shed shortly before the flower opens, but the stigma does not become receptive until soon after this time. The flowers of *Lyonia* are thus slightly protandrous. The stigma is probably receptive when a small viscid droplet is secreted at the tip of the stylar canal.

The flowers of *Lyonia* display a number of characters that are usually associated with pollination by bumblebees (*Bombus*) or other bees (see Knuth, 1909; Faegri & van der Pijl, 1972; Proctor & Yeo, 1973). The flowers are pendulous, very fragrant, and white to slightly pinkish, with cylindrical to urceolate corollas and a hidden, nectar-secreting disc (at the base of the ovary). In all species, the S-shaped and basally swollen filaments serve to hold the anthers in a ring around the style, with the pores directed inward (FIGURE 11). When the filaments are bent outward and are allowed to spring back, the pollen is discharged. The stigma is essentially at the same level as the mouth of the corolla, making the opening, in most species, so small that bees visiting the flower probably cannot fail to come into contact with it. Nectar accumulates at the base of the ovary, where it is held by the pubescence of the ovary and also by the filament bases. Pollination is accomplished when the bee's tongue brushes the curved filaments or small spurs in reaching for the nectar, thus causing pollen to be dusted on its proboscis (Lovell & Lovell, 1935; and pers. obs.). The pollen is then carried to another flower and deposited on the stigma.

Lovell and Lovell (1935) found the flowers of *Lyonia ligustrina* to be almost exclusively pollinated by bumblebees. After observing a large bush for two hours, they noted that all flowers probably received several visits. *Bombus ternarius* was quite abundant, and one individual was seen making 16 visits in one minute. On several occasions the author has seen bumblebees visiting the flowers of this species, and of *L. ferruginea* and *L. fruticosa.* The bees landed on the lower side of a flower cluster, hung onto the flowers, and took nectar from the various flowers of that cluster. The bees then flew to another inflorescence on the same or a nearby shrub (pers. obs). Robertson (1927) has observed bumblebees and other bees (and butterflies) visiting the flowers of *L. ferruginea;* scoliid wasps (*Campsomeris*) have also been seen visiting the flowers of this species (pers. obs.). The author has not seen insects visiting the flowers of any of the West Indian species, but because their floral morphology is similar to that of *L. ferruginea,* they may also be pollinated by various bees.

Lovell and Lovell (1935) covered several panicles of *Lyonia ligustrina* with a fine netting to exclude bees and other large insects. The netted panicles produced many seed capsules, although not as many as the flower clusters that had not been covered. The author has seen occasional fruits developing on isolated greenhouse plants of *L. ferruginea, L. fruticosa,* and *L. lucida,* and it is thus likely that both self- and cross-pollination occur.

ECONOMIC IMPORTANCE

The leaves of *Lyonia mariana* contain the narcotic poison andromedotoxin (a resinoid), a compound also present in several other ericaceous genera. In fact, the species received its common name, stagger-bush, because of the intoxicating effect of its leaves on sheep and cattle (Pammel, 1911; Muenscher, 1939). *Lyonia ligustrina* (Correll & Johnston, 1970; Muenscher, 1939) and *L. ovalifolia* (Sargent, 1893; Wallich, 1820; Brandis & Stewart, 1874) are also said to cause livestock poisoning. Usually the problem is greatest in early spring when the young leaves are emerging.

An infusion of the leaves of *Lyonia ovalifolia* has been employed externally in the treatment of cutaneous diseases, and the young leaves have been said to kill insects (Wallich, 1820; Brandis & Stewart, 1874; Sargent, 1893). Troup (1921) stated that plants of this species are useful in covering hill slopes (in the western Himalayas) and in thus preventing erosion. Many of the West Indian species could also be useful in erosion control and are used for fuel by the local inhabitants. All species of *Lyonia* readily sprout from the base after cutting (or fire) and provide a constant source of firewood if not overused. The leaves of *L. ovalifolia* are rolled for cigarettes by some inhabitants of the Himalayan region.

Several species of *Lyonia* have been used as ornamental shrubs, but none has become very popular. *Lyonia mariana,* with its large, white flowers, is especially beautiful but has a tendency to have a rather straggling habit. *Lyonia lucida, L. macrocalyx, L. ovalifolia, L. villosa, L. ferruginea, L. heptamera, L. rubiginosa, L. buchii, L. urbaniana,* and *L. truncata* also would make beautiful ornamentals, and more study should be directed toward their growth and culture.

To be concluded